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Forest Birds and Ecosystem Conservation in the Rocky Mountain Foothills of Alberta

by

Daniel Richard Farr



A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy

Department of Renewable Resources

Edmonton, Alberta

Fall 1995



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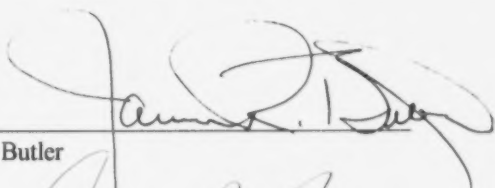
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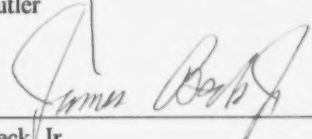
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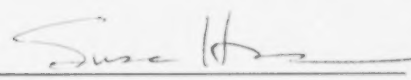
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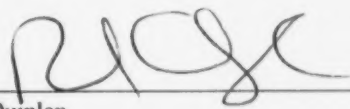
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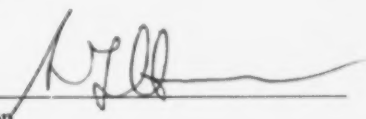
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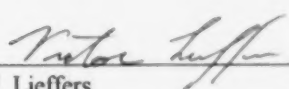

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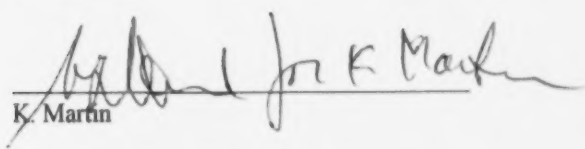

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Abstract

Among the many elements of biodiversity in boreal forest ecosystems, birds are among the most conspicuous vertebrates. Because they typically occupy particular habitats, they may be sensitive to management activities such as forestry that cause habitat change. I used point samples to estimate bird abundance in young (30 yr), mature (100 yr) and old (>180 yr) spruce-dominated forest in the Rocky Mountain foothills of Alberta during the spring of 1991 and 1992. A total of 46 bird species was observed, with an average of 5.5 species per 10 minute sample, but differences in species richness among age classes were not significant. Many species rarely were observed in any age class, but of the 10 bird species for which the statistical power to detect differences among age classes was high, all but two (Gray Jay and Yellow-rumped Warbler) differed in abundance among age classes. Only one species, Winter Wren, was observed consistently more often in old forest. As a group, permanent residents were observed more frequently in old forest, while most long-distance migrants were observed in young forest. Cluster analysis of average habitat attributes suggested that species could be grouped according to broad habitat affinities, and principal components analyses suggested that at least two species, Brown Creeper and Winter Wren, were associated with old forest habitats. Although further research is required to explain the apparent affinity of Winter Wrens and Brown Creepers for old forest, maintaining these species in this region likely will require a continued supply of old forest habitats.

I used the data from the above study plus comparable data obtained in 1990 and 1992 to test habitat suitability models for Varied Thrush, Ovenbird and Red Squirrel. Model performance varied, and the relationships between abundance and a single habitat variable were frequently obscured by correlations with other variables. Suggested revisions to each model are suggested based on the patterns observed in this study. However, conceptual problems associated with the use of habitat suitability models make it difficult to apply them to the problem of maintaining habitat diversity in managed forest ecosystems, and alternative strategies are suggested.

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1 Introduction

Among the many elements of biodiversity in boreal forest ecosystems, birds are among the most conspicuous vertebrates, although the ecological roles of birds in these systems are poorly understood. Forest birds account for only a small part of total energy flow, consuming less than one percent of net primary production (Holmes and Sturges 1973, Glowacinski and Weiner 1983). However, their effects on invertebrate population dynamics, seed dispersal, and predators such as mustelids, may be significant (DeGraaf 1978). All of the ecological processes in which temperate forest birds and other animals participate are linked to landscape-scale processes of ecosystem disturbance and forest succession, through the effects of these processes on habitat availability (Noss 1990). Many forest birds, passerines in particular, occupy particular habitats within a forest ecosystem (Telfer 1991), although the spatial pattern of variation in habitat suitability is poorly known for most species.

The limit to our current understanding of the habitat requirements of birds and other forest species places them at potential risk to management activities such as forestry that cause habitat change. Although historical processes of disturbance and succession have caused habitat change for millennia (Pielou 1991), forestry has attempted to modify these processes in order to improve the fibre production potential of the ecosystem. The suppression of forest fires attempts to reduce the role of natural disturbance processes, and new disturbances such as clearcutting have been introduced. Because of the apparent economic benefits associated with harvesting older forests and replacing them with stands of younger trees (Crossley 1985), the supply of older forests in ecosystems managed primarily for fibre production would be reduced (Hunter 1990). Maintaining habitat supply for species that require older forests is one of the major challenges facing managers attempting to integrate fibre production with biodiversity conservation (Rowe 1993).

This thesis addresses this challenge in two ways. First, Chapter 2 describes variation in habitat use by forest birds among three age classes of spruce forest in the Rocky Mountain foothills of Alberta. Forest harvesting is widespread in this region and elsewhere in Canada (Canadian Council of Forest Ministers 1992), with older stands generally scheduled for harvest before younger stands (Crossley 1978, 1985). An improved understanding of the contribution to regional biodiversity of older forest relative to younger forest would assist in conservation planning for future habitat diversity. Reid and Miller (1989) suggested that ecosystems containing a diverse range of habitats may be better able to withstand potential environmental stresses such as climate change or invasion of exotic organisms than anthropogenically simplified ecosystems. By maintaining habitat diversity in an uncertain future, forest ecosystems may also be better able to sustain a wide range of values for human societies (Franklin 1988).

The second contribution of this thesis to the challenge of integrating fibre production with biodiversity conservation is in Chapter 3, a preliminary test of habitat suitability models for three vertebrate species. Managers in the Rocky Mountain foothills are developing an approach to habitat conservation that uses habitat suitability index (HSI) models (USDI 1981) for selected vertebrate indicator species (Bonar *et al.* 1990). By linking these models existing timber supply models, it would be possible to predict the future supply of habitat for a given species under a range of alternative forest harvesting scenarios (Bonar *et al.* 1990). Among the 30 species chosen for model development, 16 were selected specifically to represent particular habitat types found in the region (Bonar *et al.* 1990). Developed using the standards of the U.S. Fish and Wildlife Service (USDI 1981), the models were based on proposed habitat relationships derived from literature reviews and specialist opinion (Quinlan *et al.* 1990). Of the 5 models proposed in 1990 (Bonar *et al.* 1990),

Chapter 3 provided a preliminary test for 3 species: Varied Thrush (*Ixoreus naevius*), Ovenbird (*Seiurus aurocapillus*) and Red Squirrel (*Tamiasciurus hudsonicus*). Each of these species was selected to represent a particular range of habitats found in the region. They, along with other models under development (Bonar, pers. comm.), are intended for use by managers attempting to integrate requirements for fibre production and habitat diversity in a managed forest ecosystem (Bonar *et al.* 1990).

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2 Forest age and the abundance of breeding birds in the Rocky Mountain Foothills of Alberta

2.1 Introduction

The distribution of many species of birds is related to vegetation structure and composition (Grinnell 1917, Lack 1933, Hildén 1965). James (1971) suggested that species occupy habitats that fall within their "niche gestalt", an innate response to vegetation and other environmental factors. For many species, these factors may form a continuous range, with unsuitable environmental conditions at both ends of the range (Bond 1957). By measuring habitat attributes in many locations, and relating them to an index of habitat suitability (*e.g.*, presence or abundance), it is possible to describe the habitat relationships of a given species (*e.g.*, James 1971, Whitmore 1975, Wiens and Rotenberry 1981, Collins *et al.* 1982, Conner *et al.* 1983, Sherry and Holmes 1985, Douglas *et al.* 1992). Extrapolations to one region from studies in other regions are of limited usefulness because many species exhibit geographic variation in habitat use (Collins 1983a, 1983b, James *et al.* 1984, Shy 1984). In order to understand the implications of regional changes in habitat supply on bird populations, site-specific information on habitat use is necessary.

Habitat structure and composition in boreal forest ecosystems have been strongly influenced by disturbance processes and subsequent successional change (Rowe and Scotter 1973, Heinselman 1981). In the Rocky Mountain foothills, large, frequent forest fires have acted to reduce the area of older forest, and the area of forest older than 150 years was less than 5% at the turn of the century (Van Wagner 1978). This proportion probably increased with elevation (Tande 1979). Despite its historical rarity throughout the western boreal region, old forest may represent the preferred habitat for many bird species (Telfer 1993), because it contains habitat conditions that are rare or absent in younger forest (Hunter 1990). Identifying species that prefer older forest is necessary before it is possible to assess the extinction risks associated with industrial forest operations, in which older forest stands are preferentially harvested before younger stands (Bonar *et al.* 1990, Hutto *et al.* 1993). Forest harvesting on an industrial scale began in the Alberta foothills in 1956, with the establishment of a forest management agreement area of approximately 800,000 ha (Crossley 1978). Drawing partly from European forestry models (Crossley 1985), the forest management system is primarily two-pass clearcutting, with management efforts directed towards achieving an even age class distribution more suitable for a continuous high yield of wood products (Crossley 1978).

In this study, I compared the species richness and abundance of breeding birds in young, mature and old spruce forests in the Rocky Mountain foothills of Alberta. I also described relationships between abundance and habitat attributes, in order to characterize the habitats occupied by different species, and illustrate patterns of similarity among species.

2.2 Study area

The study area is south of Hinton (53°25'N, 117°35'W) in the McLeod River drainage near the eastern slopes of the Rocky Mountains, in the Subalpine Forest Region (Rowe 1972). The topography is moderate to steep foothills, with elevation ranging from 1200 to 1600 m. Mature (80-120 yr) coniferous forest forms the dominant vegetation cover, with smaller proportions of both younger and older stands. Most old stands in the area are dominated by white spruce (*Picea glauca*), often in association with subalpine fir (*Abies lasiocarpa*), while most mature stands are dominated by lodgepole pine (*Pinus contorta*) or white spruce (Crossley 1978, Corns 1983). Stands dominated by deciduous species, primarily aspen poplar (*Populus tremuloides*) are uncommon except at lower elevations (Corns 1983). Most young stands were logged by clearcutting since 1956, and are highly

variable in tree species composition. In all 3 forest age classes, black spruce (*Picea mariana*) is dominant in many low relief or moist areas, and hybrid spruce (*P. glauca* X *P. engelmannii*) gradually replaces white spruce at higher elevations (Daubenmire 1974).

2.3 Methods

2.3.1 Site selection

I limited sampling to spruce-dominated stands in an attempt to minimize the differences among study sites that were not related to stand age. Nine rectangular study sites (Fig. 2.1), 3 per age class and approximately 110 ha each in size, were selected on the basis of access and dominance by a single age class of forest. Sample size was limited by the scarcity of potential sites in the old age class. Within young sites (elevation 1370 - 1470 m) at least 70% of the forest was logged between 1956 and 1958, with the remaining area logged between 1966 and 1985, or left unlogged. Mature sites (1330 - 1380 m) were covered by forest originating from fire between 1880 and 1900, with the exception of one site (M1), about 10% of which was forest originating prior to 1810. All old sites (1400 - 1510 m) were covered by forest originating from fire prior to 1810, except for one (O2) that appeared to have partially burned in the late 1800's. All silvicultural and fire history information were from records maintained by Weldwood of Canada Ltd. (Hinton Division).

2.3.2 Habitat sampling

The sample units within each site consisted of 12 circular plots, arranged in either 3 rows of 4, or two rows of 6. Unless otherwise noted, I excluded plots in young sites that contained unlogged forest from all analyses, leaving 6-8 plots in young sites, 12 plots all other sites, for a total of 93 plots included in the sample. Plot centres were approximately 300 m apart, giving a maximum non-overlapping plot radius of 150 m, an area of 7.1 ha. The sampling effort used to estimate habitat attributes varied among plots (see below), so that more heterogeneous plots were sampled more intensively. I used aerial photographs, silvicultural history maps and forest cover maps to subdivide each plot into stands of relatively homogeneous forest cover, and randomly selected one sub-plot per stand. From 1 to 6 sub-plots were sampled in each plot, during June-August 1991 or June-July 1992.

At each sub-plot location, I visually estimated forest stand characteristics using the specifications of the Alberta Vegetation Inventory (Alberta Forestry, Lands and Wildlife 1991) (Table 2.1). I also counted the number of live and standing dead trees in 6 diameter intervals within a 10x10 m square area. Although not used in analyses, I estimated total basal area by combining estimates of the cross-sectional area at breast height of all trees in each diameter interval. I also measured understorey structure below 3 m by estimating the proportion of a 0.5 m wide cloth that was obscured by coniferous or deciduous vegetation at 4 height intervals from a distance of 10 m (Table 2.1). Four estimates, one along each side of a 10x10 m square, were averaged to obtain a single value for each height interval.

One value for each habitat attribute was obtained per plot by calculating the mean of all sub-plots in the plot, weighted by the relative area of the stand in which the sub-plot was located. Some habitat attributes were combined prior to analysis in order to simplify presentation and improve accordance with statistical assumptions of normality.

2.3.3 Bird sampling

I sampled birds in each site using point samples (Reynolds *et al.* 1980) in spring 1991 and 1992, and one observer (Farr) conducted all bird sampling. I divided the sampling season into 4 two-week intervals between 15 May and 15 July, and sampled each site once during each interval in 1991, and once during the middle two intervals (*i.e.*, June) in 1992. Sample dates for each site in June 1992 differed by less than 5 calendar days from corresponding sample dates in June 1991. I sampled on days with little or no rain and winds less than 20 km/h, beginning one half-hour before local sunrise (approximately 0500 h MST), and ending 4.5 hours later. I varied the order in which the 12 plots in each site were visited, so that each plot was visited in early, mid- and late morning. Sample times for each plot in June 1992 were within 30 minutes of the sample times in June 1991.

At each plot, I counted all birds observed (seen or heard) from the plot centre within a 10 minute period. I also estimated the distance to each bird when first observed, and those judged to be more than 150 m away were excluded from analyses. I also excluded birds observed flying overhead unless they also were observed on the ground or vegetation. Because mature and old sites were surrounded on all sides by mature or old forest, underestimating distance potentially had a greater affect on sampling results from young sites, all of which had mature forest along at least one side.

2.3.4 Analysis

2.3.4.1 Age class comparisons

I compared habitat attributes and bird species richness and abundance among forest age classes using sites ($n = 3$ per age class) as the sample unit. Pooling the 36 plots in each age class would have improved statistical power through increased sample size, but sites, not plots, were the appropriate sampling unit replicated within each age class (Hurlbert 1984, Eberhardt and Thomas 1991). Because the sites were not randomly selected from a larger number of sites, inferences apply to the particular sites sampled (James and McCulloch 1985), although they did not appear to be unusual relative to similar-aged stands in the region.

I compared the habitat attributes of the 3 age classes using the mean values for each site in a one-way analysis of variance (ANOVA). The results of this analysis were identical to those from a fixed-effects nested ANOVA with sites nested within age classes. While the latter test would permit an assessment of the variability among sites within age classes, the distribution within sites of most habitat attributes was strongly skewed, and transformations frequently did not improve normality. These two problems made such an assessment inappropriate. For each analysis, I also estimated the minimum power (Toft and Shea 1983, Peterman 1990) to correctly reject the null hypothesis of no differences among age classes at an alpha-level (Type I error probability) of 0.05. I calculated power for a specific difference among age classes (Neter and Wasserman 1974, Smith *et al.* 1993), set at $\pm 50\%$ of the overall mean, based on the method given by Zar (1984:174):

$$\phi = \sqrt{[(k - 1)(MS_{\text{age}} - MS_{\text{error}}) / (k \times MS_{\text{error}})]}, \text{ where}$$

ϕ = non-centrality parameter, converted to power using appropriate power curve (Zar 1984:658),

k = number of age classes (=3),

MS_{age} = mean-square among age classes for the case where one age class equals the overall mean, and the other 2 equal 50% less than and greater than the overall mean (Neter and Wasserman 1974),

MS_{error} = mean-square error.

I expressed power as high (>80%), moderate (40-80%) or low (<40%). High power, combined with non-significant ($p>0.05$) variation among age classes, was used as the criterion for stating that no differences existed among ages. I also performed multiple comparisons (Tukey test, Day and Quinn 1989) to assess which age classes were different if variation among ages was significant ($p<0.05$)

I compared bird species richness and abundance among age classes using repeated measures ANOVA (Snedecor and Cochran 1980, SAS Institute Inc. 1989, Bergerud 1991). To permit comparisons between 1991 and 1992, I combined the 6 visits into 3 sampling sessions: May/July 1991, June 1991, June 1992. (These sessions were chosen to permit comparisons between years using samples from the same month.) For each session I calculated the mean number of species or individuals observed / plot / visit. I also performed 2 statistical contrasts: June 1991 vs. June 1992 (Year), and June '91 vs. May/July 1991 (Season). The latter contrast compares periods of high and low detectability, because many migratory species are most easily detected during June, when vocalization frequency was highest, and less easily detected in May and July (pers. obs.). I also estimated minimum power to detect differences among age classes using the methods described above, adjusted for the repeated measures design by multiplying both mean-squares by 3.

2.3.4.2 Comparisons of bird assemblages

I compared the bird species assemblages of the 9 sites using Morisita's index of similarity (Morisita 1959). Compared to other similarity indices, Morisita's index is unaffected by sample size, except when sample size is very small, and it is strongly influenced by the most frequently observed species in each site (Wolda 1981). In this study Morisita's index represents the probability that 2 observations, one from each of 2 sites, are the same species, relative to the probability that 2 observations from either site alone are the same species (Krebs 1989:306). Morisita's index ranges from 0 (not similar) to about 1 (very similar), and the formula is as follows:

$$C = 2 \times \sum (X_{ij} \times X_{ik}) / [(L_j + L_k) \times N_j \times N_k], \text{ where}$$

$$C = \text{Morisita's index of similarity between sites } j \text{ and } k$$

$$X_{ij}, X_{ik} = \text{number of observations of species } i \text{ in sites } j \text{ and } k$$

$$N_j = \sum X_{ij} = \text{total number of observations in site } j$$

$$N_k = \sum X_{ik} = \text{total number of observations in site } k$$

$$L_j = \sum [X_{ij} (X_{ij} - 1)] / [N_j (N_j - 1)]$$

$$L_k = \sum [X_{ik} (X_{ik} - 1)] / [N_k (N_k - 1)]$$

I also used unweighted pair-group (UPGMA) cluster analyses (Romesberg 1984), to determine whether patterns of similarity in bird abundance matched those based on habitat attributes. In the first analysis, bird abundance in each site was estimated by the mean number of observations / plot / visit (*i.e.*, counts adjusted for sampling effort). I used the chi-square measure of dissimilarity, first standardizing the abundance of each species to range between 0 and 1. In the second analysis, I determined similarity among sites based on the mean habitat attributes of each site, using squared euclidian distances as the measure of dissimilarity, standardizing each attribute to a mean of 0 and standard deviation of one (*i.e.*, z-scores).

2.3.4.3 Associations between birds and habitat

In the remaining analyses, I used individual plots as the sample units in order to relate habitat attributes to bird distribution and abundance. I estimated average habitat attributes for each bird species by calculating the mean of each attribute for all plots in which a species was observed,

weighted by the number of observations per plot. I summarized patterns of similarity among species using UPGMA cluster analysis, with squared euclidian distances as the measure of dissimilarity, first standardizing each attribute to z-scores.

Because many habitat attributes were highly intercorrelated, describing habitat use by associating bird abundance with single habitat attributes was inappropriate (Johnson and Wichern 1988). I therefore used principal components analysis (PCA) to construct a set of new, uncorrelated habitat factors which accounted for a known proportion of the variability among the original habitat attributes (Johnson and Wichern 1988). Within the context of this multivariate habitat "space", I related the number of observations in a plot to the habitat attributes of that plot (see Rotenberry and Wiens 1980). First, I summarized the habitat differences among sites using the correlation matrix of the 18 habitat attributes measured in each sample plot. Prior to this analysis, I transformed any habitat attributes that were not normally distributed, using either arcsin or log transformations (Krebs 1989). To improve the interpretability of the resulting factors, varimax rotation was used to minimize the number of attributes that were strongly correlated with a single factor (Norusis 1992). I interpreted factors by inspecting their correlations, or loadings, with the original 18 habitat attributes. Differences among sites were illustrated using mean values of each habitat factor for each site, and I summarized the habitat associations of each bird species by calculating Spearman's rank correlations between each habitat factor and the number of observations per plot (Rotenberry and Wiens 1980).

For comparative purposes, I also summarized the habitat associations of bird species directly, by performing a PCA of the average habitat values for each species. Mean habitat values for each species were weighted by the relative number of observations in each plot, and sample size for each species ranged from 12 to 93 plots. A PCA was performed on the correlation matrix of mean habitat attributes as described above, except that because most habitat attributes were normally distributed, no transformations were done.

2.4 Results

2.4.1 Age class comparisons

2.4.1.1 Habitat attributes

The power to detect differences as large as 50% of the overall mean was low for all but 8 of the 20 habitat attributes tested (Table 2.2), and only tree height and density of large live trees differed significantly among age classes (Table 2.2). Variation among sites within age classes (nested ANOVA, not shown) was significant for almost all habitat attributes, but larger sample size (9 sites, 93 plots) contributed to the relatively high power (>80%) of such tests.

2.4.1.2 Bird species richness

A total of 46 bird species was observed within 150 m of sample plot centres, and several other species were observed only beyond 150 m (Common Loon, Ovenbird, Northern Waterthrush) or as they flew overhead (Great Blue Heron, Canada Goose, Osprey, American Crow, Brown-headed Cowbird, Evening Grosbeak). A complete list of birds observed, with scientific names, is given in Appendix 1, and raw data are contained in Appendix 2.

The 3 forest age classes contained between 30 and 36 species each, with no large differences in total species richness among ages. The young age class contained 36 species, with 4 (Olive-sided Flycatcher, Magnolia Warbler, Pine Siskin, White-winged Crossbill) observed only in plots containing some unlogged forest; each of these species was observed fewer than 4 times. A total of

35 and 30 species were observed in mature and old age classes, respectively. In all age classes, total species richness was dominated by species that were rarely observed, with most (53-57%) of the species in each age class having a combined total of less than 5% of all observations.

I also tallied the number of species observed per site, per plot, and per visit to each plot, and in all 3 cases, differences among age classes were not significant (Table 2.3). Power analyses suggested that moderate differences ($\pm 50\%$) among age classes had a high probability of being detected for each of these measures of species richness. In addition, repeated measures ANOVA indicated that the number of species / plot / visit did not differ significantly between years ($F_{1,6} = 0.29$, $p=0.609$), but more species were observed in June 1991 compared to May/July 1991 ($F_{1,6}=39.83$, $p=0.001$) (Table 2.3). Within the young age class, nested ANOVA suggested that there were no differences between plots containing no unlogged forest and those containing some unlogged forest in either number of species / plot ($F_{3,30}=1.84$, $p=0.162$) or number of species / plot / visit ($F_{3,30}=0.52$, $p=0.675$).

2.4.1.3 Individual bird species

Over half (25) of the 46 species were observed most frequently in young sites, 12 were most frequently observed in mature sites, and 9 were most frequently observed in old sites. However, absolute differences among ages often were small, partly due to the low frequency with which many species were observed. I attempted to control the reliability of abundance estimates in each age class by excluding all species observed in fewer than 10 plots. Of the remaining 25 species, the abundance of 8 varied significantly ($p<0.05$) among age classes (Table 2.4). For 3 of these (Red-breasted Nuthatch, Golden-crowned Kinglet, White-winged Crossbill), the effect of age varied among sampling sessions (significant interaction between age and session terms in ANOVA), but all 3 species were seldom if ever observed in young forest (Table 2.4). Of the remaining 5 species, multiple comparisons suggested that Winter Wrens were more abundant in old forest than either young or mature forest, while Warbling Vireos, Orange-crowned Warblers, White-throated Sparrows, and Lincoln's Sparrows were all more abundant in young forest than either mature or old forest (Table 2.4). Power analyses indicated that Gray Jays and Yellow-rumped Warblers probably did not differ greatly in abundance among age classes (age effect not significant, power $> 80\%$), but for most species, the power to detect differences among ages was low or moderate (Table 2.4).

Contrasts between years and between seasons suggested that seasonal differences in abundance were usually greater than annual differences. Only 2 species (Ruby-crowned Kinglet, Orange-crowned Warbler) were observed more frequently in one year (1991) compared to the other (Table 2.4). In contrast, the abundance of 8 species differed between June 1991 and May/July 1991; all but one of these (White-winged Crossbill) were observed more frequently in June 1991 (Table 2.4).

2.4.1.4 Ecological groups

The number of birds observed in each forest age class was related to migratory pattern, foraging mode and nest location, although the 3 categories were not mutually independent. For example, of the 7 cavity nesting species, all but one (Northern Flicker) were permanent residents, and 11 of the 14 species nesting in coniferous trees were foliage gleaners (Appendix 2.1). While the abundance of short-distant migrants did not differ among forest ages, permanent residents were observed more frequently in the old age class, and long-distance migrants were observed most frequently in young sites (although the effect of age varied among sampling sessions, Table 2.5). Of

the 4 categories of foraging mode, ground gleaners were more common in young sites, bark gleaners were more common in old sites, while foliage gleaners did not differ in abundance among ages. Finally, birds that nested on the ground or in deciduous trees were more common in young sites than in either mature or old sites (Table 2.5). In contrast, cavity nesters were much more common in old sites, while species nesting in coniferous trees did not differ in abundance among ages.

2.4.2 Comparisons of bird assemblages

The bird assemblages in the mature and old age class were more similar to each other than either was to the young age class. Morisita's index of similarity, calculated for each of the 36 possible pairs of sites, averaged 0.91 between mature and old sites ($n = 9$ site pairs), while young sites were less similar to either mature sites (0.77, $n = 9$) or old sites (0.72, $n = 9$). Comparisons within each age class suggested that assemblages in young sites were more variable (mean Morisita's index = 0.88, $n = 3$ site pairs) than either mature sites (mean = 0.94, $n = 3$) or old sites (mean = 0.95, $n = 3$).

These results were supported by a cluster analysis using the chi-square measure of dissimilarity. Based on standardized counts of each bird species, young sites formed a group that was distinct from mature and old sites, but there was no clear separation between mature and old sites (Fig. 2.2). The apparent distinctness of bird assemblages in young forest was not consistent with patterns of similarity in habitat attributes. A second cluster analysis (Fig. 2.2) suggested that the habitat attributes in one young site (Y3) were distinct from all other sites, with the pattern of similarity among the remaining sites having no clear relationship to stand age.

2.4.3 Associations between birds and habitat

The cluster analysis of average habitat attributes separated bird species into 5 groups (Fig. 2.3), which were interpreted as follows. Group 1 contained primarily species that were frequently observed in all 3 age classes, including the 2 species (Gray Jay, Yellow-rumped Warbler) that previous analyses (Table 2.4) suggested were habitat generalists. Group 2 was composed of species that were much more frequently observed in mature and old forest compared to young forest. Group 3 contained species with an apparent affinity for young forest, and included 3 of the 4 species observed significantly more often in young forest compared to mature or old forest (Table 2.4). Species in Group 4 also tended to be more common in young forest compared to mature or old forest, but were not as limited to young sites as the previous group. Finally, Group 5 contained 2 species, including the only species (Winter Wren), that was consistently observed significantly more often in old forest compared to mature or young forest (Table 2.4).

In order to further clarify the habitat relationships of each bird species, I summarized the 18 habitat attributes measured in 93 sample plots using principal components analysis. Three new habitat axes that together accounted for 59% of the variation among the original variables (Table 2.6) are interpreted as: a transition from plots with relatively little deciduous understorey cover to those with a relatively dense deciduous understorey (PC 1); a second axis reflecting the development of young vs. old forest structure (PC 2); and a third axis representing the degree of black spruce dominance (PC 3). The positions of the 9 study sites in relation to these 3 habitat axes (Fig. 2.4) reflected the overlap among age classes suggested by cluster analysis (Fig. 2.2), but also indicated major sources of variation within each age class. Young sites differed primarily in the degree of deciduous understorey cover, indicated by their spread along PC 1. One of the 3 mature sites (M3) differed from the other 2 in having a habitat structure more typical of young forest (low PC 2)

combined with dominance by black spruce (high PC 3). Habitats in the 3 old sites were more uniform, with some variation associated with deciduous understorey cover and the development of young vs. old forest structure (PC 1 and PC 2).

When the values of PC 1, PC 2 and PC 3 were correlated with the number of observations in each plot, habitat relationships could be illustrated for 24 bird species. For the remaining species, the number of observations per plot was not significantly ($p < 0.05$) correlated with any of the 3 principal components. As indicated by Fig. 2.5, the 5 groups of species formed by cluster analysis (Fig. 2.3) occupied different parts of the habitat space defined by principal components 1-3, although the groups were not entirely distinct. The interpretation of habitat relationships for each group generally followed that given above. Group 1 occupied the middle portion of the habitat spectrum, but included species such as Yellow-rumped Warbler and Gray Jay that occurred in almost all of the plots sampled. Group 2 had more affinity to plots with old forest structures. Groups 3 and 4 were observed most frequently in habitats without old forest structures, with the latter group strongly associated with plots having dense deciduous understorey cover. Finally, both species in Group 5 were associated with plots containing old forest structures and little deciduous understorey cover.

The patterns suggested by this analysis were generally supported by the results of a second principal components analysis (Table 2.7) based on weighted mean habitat values for each bird species. The interpretation of habitat relationships for the 5 species groups from this second analysis (Fig. 2.6) were similar to those suggested by the first PCA.

2.5 Discussion

2.5.1 Patterns of habitat use

This study suggested that the bird assemblages in mature and old spruce forest were generally more similar to each other than either was to young forest. Although not significant, young forest may have contained more species, and certain groups of species had strong affinities for either young or old forest (Table 2.5). These assemblage comparisons, however, do not provide information on the distribution or abundance of individual species (James and Rathbun 1981). Only 8 species differed significantly in abundance among age classes, although the power to detect age-related differences was low for most other species. However, cluster and principal components analyses identified groups of species with affinities to particular habitat conditions. This suggests that many birds occupied a specific range of habitats, but that stand age may not be the dominant environmental attribute influencing distribution. For many habitat attributes, differences among age classes were small, although the power to detect differences among age classes was low for most attributes (Table 2.2). Other environmental factors such as moisture and nutrient availability, topography, elevation, and the nature of past disturbances all have potentially large influences on vegetation structure and composition (Corns 1983). For example, the presence of characteristic plant species indicated that one mature site (M3) was dominated by a *Picea mariana* / *Ledum* / *Equisetum* ecosystem association, while the other 2 were predominantly *P. glauca* / *Hylocomium*, with lower soil moisture and higher nutrient availability (Corns and Annas 1986). This difference is reflected in the relatively distinct habitat and bird assemblage of site M3 compared to the other 2 mature sites (Fig. 2.2). The influence of soil properties, particularly moisture, on bird distributions is probably significant (Smith 1977, Douglas *et al.* 1992), and may exceed that of disturbance history. The analysis presented in Appendix 3 represents a preliminary attempt to summarize bird distributions along ecological gradients in mature and old sites.

Differences in the prevalence of canopy gaps (observed on 1:20,000 air photos) among mature and old sites also may have contributed to variations in bird abundance. Canopy gaps usually were present in low-lying areas in which black spruce often was dominant; gaps with less than 30% canopy closure accounted for 3-25% of the area of each site. They may explain the presence in mature and old sites of species that were observed much more frequently in young sites (e.g., Hermit Thrush, White-throated Sparrow).

Silvicultural prescriptions probably contributed to habitat differences within the young age class. For example, small patches of seed trees were maintained within one of the young sites (Y3) for 15 years after harvesting. This probably caused the very high density of small live trees and dense coniferous understorey cover, contributing to a bird assemblage that was distinct from the other 2 young sites (Fig. 2.2). Other silvicultural treatments such as thinning (Szaro and Balda 1979, Kilgore 1971), removal of competing vegetation (Morrison and Meslow 1984), site preparation, planting, and leaving advance regeneration, may also result in bird assemblages that differ among stands that are similar in age.

Because of the above factors, the sites sampled cannot be considered "typical" successional sequences, although in the absence of fire, a range of forest types frequently converge to become dominated by white spruce and fir (Oosting and Reed 1952, Day 1972, Rowe and Scotter 1973, Kelsall *et al.* 1977, Romme and Knight 1981, Corns and Annas 1986). Restricting sample sites to a narrower range of ecosystem associations may have improved the degree to which differences among age classes reflected likely successional changes.

The 5 species groups formed by cluster analysis (Fig. 2.3) represent species that share common habitat affinities, and there is no evidence that they represent discrete communities *per se* (Collins *et al.* 1982). Studies of the geographical ecology of Wood Thrushes (*Hylocichla mustelina*) indicate that throughout its breeding range in eastern North America, it co-occurs with a shifting assemblage of closely related sympatric species (James *et al.* 1984), and the most appropriate model for explaining its distribution may be that of Grinnell (1917). Grinnell suggested that the distribution pattern of a species is a function of a unique suite of adaptations for a particular range of environmental conditions (James *et al.* 1984). A species is able to occupy habitats that are within this range of tolerance, and competition may play only a minor role. Grinnell's hypothesis is supported by the highly individualistic changes in North American plant and animal distributions in response to climate change during the past 18,000 years (Hunter 1992). As a result, "communities" of birds, particularly in boreal regions, may be more accurately viewed as transitory assemblages of species with similar environmental tolerances (Hunter 1992).

The habitat relationships suggested by principal components analysis (Figs. 2.5, 2.6) represent hypotheses for further investigation, rather than definitive patterns (Morrison *et al.* 1992). The primary purpose of PCA was to suggest relationships among many intercorrelated variables that would not be obvious from repeated univariate analyses. The method is sensitive to the choice and range of habitat attributes included (James 1971:234, Johnson and Wichern 1988), and results may vary among locations with different habitat correlations (Collins 1983b). Results of PCA often are overinterpreted (James and McCulloch 1990), despite evidence that the procedure can extract apparently reasonable patterns from random data (Karr and Martin 1981, Rexstadt *et al.* 1988). In addition, the portrayal of a species's mean position in PCA habitat space (Fig. 2.6) did not distinguish habitat generalists from species that occupied a smaller range in the middle of the habitat spectrum. Concentration ellipses (e.g., Smith 1977, Collins *et al.* 1982), or contours of species

abundance (Rotenberry and Wiens 1981) would illustrate differences in habitat niche breadth, but are limited to 2 principal components.

One hypothesis suggested by PCA is whether or not dense deciduous understorey cover is an important habitat requirement for Ruffed Grouse, Yellow-bellied Flycatcher and Tennessee Warbler (Group 4 species), as suggested by their positions in the derived habitat space (Figs. 2.5, 2.6). If such cover is an important habitat requirement, then "free-to-grow" vegetation management that releases crop trees from competing deciduous vegetation would reduce habitat quality for these species. Removal of shrubs around Ruffed Grouse drumming logs in Alberta rendered them unsuitable (Boag 1976), and manual and chemical shrub removal in southern Norway clearcuts reduced bird densities significantly (Slagsvold 1977). Monitoring populations and reproductive success before and after vegetation management in treatment and control areas would provide a test of this hypothesis.

Additional studies are also required to clarify the role of older forest in maintaining populations of Winter Wrens and Brown Creepers. In this study, Winter Wrens were observed significantly more frequently in old forest (Table 2.4), and the habitats occupied by Winter Wrens and Brown Creepers were very similar (Fig. 2.3). Both species appeared to be associated with habitats containing old forest structure and relatively little deciduous understorey cover (Figs. 2.5, 2.6). More extensive sampling in this region (Chapter 3) and elsewhere in the northern Rockies (Holroyd and Van Tighem 1983) support the hypothesis that these species occur primarily in old forest habitats dominated by white spruce and subalpine fir. Without experimental habitat manipulations, explanations for this pattern must be speculative (Cale *et al.* 1989), but the natural history of each species suggests that the densities of dead trees and large trees may influence their distributions.

Brown Creepers build stick nests in tree crevices, usually behind loose bark on standing dead trees (Davis 1978, Peck and James 1987). During this study I located 2 Brown Creeper nests; both were in site O3, behind loose bark in standing dead white spruce trees (45 and 56 cm dbh) in advanced stages of decay. Although not statistically significant, the densities of medium and large dead trees were relatively high in old sites, and perhaps suitable nest trees are scarce in other habitats. However, the hypothesis that nest site availability limits population sizes of secondary cavity nesters (von Haartman 1956) is not supported for all species (Brawn and Balda 1988), and other factors such as food availability may be more important.

The feeding behaviour of Brown Creepers, which glean arthropods from the surface of tree bark (Franzreb 1985, Morrison *et al.* 1987, Adams and Morrison 1993) may be a more important limiting factor than nest location. Mariani and Manuwal (1990) found that the abundance of bark-dwelling arthropods on Douglas-fir (*Pseudotsuga menziesii*) in Washington increased with trunk diameter, probably because of a concomitant increase in bark fissure depth (Lundquist and Manuwal 1990). This increased food availability may explain why Brown Creepers spent more time foraging on large (>50 cm dbh) Douglas-fir trees compared to smaller ones (Lundquist and Manuwal 1990). Energy efficiency may be important for a small, trunk-climbing bird (Norberg 1986 [*Certhia familiaris*]), and perhaps Brown Creepers are able to forage more efficiently in habitats containing many large trees. This hypothesis was suggested by Keller and Anderson (1992) to explain the absence of Brown Creepers in strip-cut and spot-cut stands compared to unfragmented tracts of subalpine forest in Wyoming.

The association of Winter Wrens with old forest habitats may be indirectly related to the densities of large live trees and dead trees. Winter Wrens usually nest on or near the ground, often

among the roots of fallen trees or other coarse woody material (Peck and James 1987). Foraging activity is also concentrated among fallen logs and other structures close to the ground (Sabo 1980, Van Horne and Bader 1990). Although I did not measure the density of fallen coarse woody material in this study, higher densities of large live trees and standing dead trees in old forest may be correlated with higher densities of coarse woody material on the forest floor. Titterton *et al.* (1979) found that Winter Wren abundance was positively correlated with density of coarse woody debris, possibly explaining why they are relatively common in recent clearcuts in Maine spruce/fir forests (Titterton *et al.* 1979, Hunter 1992). In west-central Alberta, Winter Wrens are not known to occur in recent clearcuts (R. Bonar and D. Farr, unpubl. data), perhaps because of lower densities of coarse woody debris on the ground.

2.5.2 Management implications

Further studies are required to determine if the patterns described in this chapter are consistent elsewhere in the region. However, apparent preference for older forests by Winter Wrens and Brown Creepers is consistent with what is known of their feeding and nesting ecology. In order to maintain viable populations of these and other vertebrates preferring older forest in regions managed primarily for fibre production, an adequate supply of older forest habitats would be necessary. Rotation intervals of 80 years (Crossley 1978, Walker 1990) act to maintain older stands in low supply, possibly producing a shortage of habitats for species requiring old forest. Occasionally lengthening rotation age on part of the land base (Harris 1984, Hunter 1990:69, 1993), and would be analogous to the escape from fire by parts of this historically fire-disturbed landscape (Van Wagner 1978). Old forest could appear and disappear in different locations, resulting in periodic colonizations and extinctions consistent with the "winking patches" concept of Wilson (1975:107).

The appropriate number and arrangement of old forest patches at any one time probably varies considerably for different bird species because of differences in rates of reproduction and dispersal (Simberloff and Abele 1982). However, Urban and Shugart (1986) suggested that most bird populations in habitat mosaics probably are limited by net reproduction rather than dispersal abilities (but see Fritz 1979, Barrowclough and Coats 1985). If so, then the presence of a small number of high quality habitat patches, in which many surplus individuals are produced, would be better than many patches of lower quality (Gilpin and Soulé 1986, Gilpin 1987). Populations in high quality patches may also be more stable, and less prone to chance extinctions (Wiens 1989:173, Thomas *et al.* 1990).

At the scale of individual patches, many silvicultural options exist to increase the future value of regenerating cutblocks to species that require old forest structures (Hunter 1990). Historically, large differences in fire intensity (Rowe and Scotter 1973) created a larger range of post-disturbance habitats than those created by clearcutting (Hunter 1990). Some practices, such as retaining clumps of standing live and dead trees (Raphael and White 1984) and piles of coarse woody debris in recent clearcuts, may increase habitat supply for species that use old forest structures by increasing the suitability of post-disturbance habitats, or accelerating the development of suitable habitats later in the rotation. Promoting the establishment of white spruce and subalpine fir rather than lodgepole pine, and artificially increasing the densities of standing dead trees by killing mature live trees (Bull and Partridge 1986) also may increase habitat supply for species dependent on large trees and standing dead trees. Deciding on appropriate snag densities is a difficult problem (Hunter 1990), but the density of standing dead trees >15 cm dbh in the old stands sampled in this

study ranged from 38-211 per ha (Table 2.2). As in another study (Stelfox 1988), large snags (>35 cm dbh) were much less common (0-50 per ha) than smaller snags.

A conservative approach (Hunter 1990:67) to forest habitat management may be necessary to avoid unexpected population declines of species such as Winter Wrens and Brown Creepers. In north Finnish spruce and pine forests, extensive harvesting and thinning of mature and old forest (Kuusela 1972) probably caused reductions in populations of many bird species (Järvinen *et al.* 1977), including Three-toed Woodpecker, Common Treecreeper (*Certhia familiaris*), Bohemian Waxwing and Pine Grosbeak (Helle and Järvinen 1986, Virkkala 1991). The declines for many species were proportionately greater than the reduction in the area of old forest (Järvinen and Väisänen 1979), and they will either successfully pass through population bottlenecks or suffer local extinctions. Interestingly, all of these species are permanent residents that, as a group, were more abundant in the old forest sampled in this study (Table 2.5). Despite the recent emphasis on neotropical migrants (*e.g.*, Hagan and Johnston 1992, Finch and Stangel 1993), permanent residents may be more sensitive to forestry operations in boreal landscapes (Hunter 1992), and deserve increased attention.

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Table 2.1. Habitat attributes measured at each sub-plot location in 3 age classes of forest in west-central Alberta.

Habitat Attribute	Description
AVI^a Attributes	
Tree Crown Closure (%)	Percent of ground covered by a vertical projection of dominant and co-dominant tree crowns, estimated to the nearest percentage category (0-5%, 6-30%, 31-50%, 51-70%, 71-100%; midpoint of each category used in calculating plot means)
Tree Height (m)	Average height ^b of dominant and co-dominant trees
Tree Species Composition (%)	Percent contribution of each canopy tree species to crown closure, in 10% intervals
Shrub Crown Closure (%)	Percent of ground covered by a vertical projection of shrub crowns.
Shrub Height (m)	Average height of shrubs, to nearest m
Live & Standing Dead Trees	
5-14.9 cm	Number of trees in each dbh ^c interval within a 10x10 m square
15-24.9 cm	
25-34.9 cm	
35-44.9 cm	
45-54.9 cm	
55-64.9 cm	
Understorey Structure (%)	
0.0-0.5 m	Percentage of a cloth obscured by coniferous or deciduous vegetation from a horizontal distance of 10 m
0.5-1.0 m	
1.0-2.0 m	
2.0-3.0 m	

^a Alberta Vegetation Inventory (Alberta Forestry, Lands and Wildlife 1991)

^b Measured with a Sunto clinometer

^c Diametre at breast height

Table 2.2. Habitat attributes of 3 age classes of forest in west-central Alberta.

n = 3 sites in each age class. Age = results of one-way ANOVA.

Power = minimum probability of rejecting the null hypothesis of no difference among age classes if $p=0.05$ and age classes differed by 50% above and below the overall mean. H = high (>80%), M = moderate (40-80%), L = low (<40%).

	Young	Mature	Old	Age		
	mean $\pm$ SD range	mean $\pm$ SD range	mean $\pm$ SD range	F (df=2,6)	P	Power $\pm$ 50%
Tree canopy						
White Spruce (%)	24 $\pm$ 13 13 - 37	35 $\pm$ 25 7 - 55	61 $\pm$ 4 57 - 66	4.24	0.071	M
Black Spruce (%)	3 $\pm$ 5 0 - 8	34 $\pm$ 37 7 - 76	10 $\pm$ 14 0 - 27	1.50	0.296	L
Subalpine Fir (%)	41 $\pm$ 29 11 - 67	3 $\pm$ 2 1 - 5	24 $\pm$ 10 14 - 34	3.62	0.093	L
Lodgepole Pine (%)	22 $\pm$ 13 12 - 37	28 $\pm$ 18 12 - 47	4 $\pm$ 5 0 - 10	2.70	0.146	L
Poplar spp. (%)	8 $\pm$ 8 0 - 16	0 $\pm$ 1 0 - 1	0 $\pm$ 0 0 - 0	2.79	0.156	L
Crown closure (%)	40 $\pm$ 1 39 - 41	49 $\pm$ 8 39 - 55	48 $\pm$ 8 41 - 57	1.72	0.257	H
Height (m)	6 $\pm$ 2 4 - 7	17 $\pm$ 2 16 - 19	22 $\pm$ 4 18 - 26	29.45	0.001	H
Live trees						
5 - 15 cm (#/ha)	1783 $\pm$ 1073 987 - 3004	1202 $\pm$ 1130 401 - 2495	458 $\pm$ 357 174 - 858	1.55	0.286	L
15 - 35 cm (#/ha)	185 $\pm$ 100 73 - 264	486 $\pm$ 194 331 - 703	430 $\pm$ 124 350 - 573	3.66	0.091	M
> 35 cm (#/ha)	0 $\pm$ 0 0 - 0	46 $\pm$ 24 22 - 70	88 $\pm$ 41 48 - 129	7.76	0.022	H

	Young	Mature	Old	Age		
	mean $\pm$ SD range	mean $\pm$ SD range	mean $\pm$ SD range	F (df=2,6)	P	Power $\pm$ 50%
Dead trees						
5 - 15 cm (#/ha)	20 $\pm$ 12 9 - 33	145 $\pm$ 105 52 - 258	104 $\pm$ 49 72 - 160	2.70	0.146	L
> 15 cm (#/ha)	28 $\pm$ 17 17 - 47	36 $\pm$ 18 16 - 50	121 $\pm$ 86 38 - 211	3.00	0.125	L
Shrubs						
Crown closure (%)	32 $\pm$ 14 17 - 45	37 $\pm$ 18 23 - 57	28 $\pm$ 3 24 - 30	0.47	0.612	M
Height (m)	1.7 $\pm$ 0.6 1.3 - 2.4	1.8 $\pm$ 0.9 1.0 - 2.7	1.4 $\pm$ 0.5 0.9 - 1.9	0.37	0.706	M
Coniferous understorey cover						
< 1 m (%)	45 $\pm$ 36 18 - 86	25 $\pm$ 9 15 - 31	41 $\pm$ 17 31 - 61	0.58	0.589	L
1 - 3 m (%)	42 $\pm$ 26 25 - 71	26 $\pm$ 6 20 - 32	24 $\pm$ 9 18 - 34	1.08	0.396	L
Deciduous understorey cover						
< 1 m (%)	30 $\pm$ 26 4 - 55	32 $\pm$ 17 15 - 50	18 $\pm$ 14 6 - 34	0.43	0.668	L
1 - 3 m (%)	18 $\pm$ 18 2 - 37	15 $\pm$ 15 1 - 30	5 $\pm$ 7 0 - 12	0.72	0.525	L
Basal area						
Live trees (m ² /ha)	25 $\pm$ 7 18 - 32	40 $\pm$ 13 32 - 55	40 $\pm$ 2 37 - 42	3.06	0.121	H
Dead trees (m ² /ha)	2.1 $\pm$ 1.1 0.9 - 3.0	3.0 $\pm$ 1.3 1.7 - 4.4	9.9 $\pm$ 7.7 2.6 - ###	2.60	0.154	L

Table 2.3. Species richness of birds in 3 age classes of forest in west-central Alberta.
 n = 3 sites in each age class. Age = results of ANOVA (see footnotes).
 Power = minimum probability of rejecting the null hypothesis of no difference
 among age classes if $p=0.05$ and age classes differed by 50% above and
 below the overall mean. H = high (>80%).

		Young	Mature	Old	Age		
		mean $\pm$ SD range	mean $\pm$ SD range	mean $\pm$ SD range	F (df=2,6)	P	Power $\pm$ 50%
Species / site	¹	28.0 $\pm$ 5.6 22 - 33	25.0 $\pm$ 1.0 24 - 26	21.7 $\pm$ 3.1 19 - 25	³ 2.19	0.194	H
Species / plot	²	14.8 $\pm$ 1.9 12.2 - 16.4	11.8 $\pm$ 1.3 10.9 - 11.1	13.3 $\pm$ 1.0 12.3 - 14.3	³ 3.12	0.118	H
Species / visit	²	6.4 $\pm$ 0.6 5.4 - 7.0	4.8 $\pm$ 1.1 4.0 - 6.1	5.2 $\pm$ 0.6 4.7 - 5.9	⁴ 3.48	0.099	H

¹ Site totals include plots containing unlogged forest; mean = 25.3 (range 21-29) when such plots are excluded.

² Site means exclude plots containing unlogged forest.

³ One-way ANOVA

⁴ Repeated measures ANOVA, interaction term not significant.

Table 2.4. Number of birds observed, by species, in 3 age classes of forest in west-central Alberta.

Units are number of observations / plot / visit. $n = 3$ sites per age class. Age and Year are from repeated measures ANOVA, with mean number of observations in 3 sessions (May/July 1991, June 1991, June 1992) as the repeated measure.

Year = result of contrast between June 1991 and June 1992 (session effect not shown).

(Interaction) = significant ($p < 0.05$) interaction between age and session terms.

(Season) = significant ($p < 0.05$) contrast between May/July 1991 and June 1991.

Power = minimum probability of rejecting the null hypothesis of no difference among age classes if $p = 0.05$ and age classes differed by 50% above and below the overall mean.

H = high (>80%), M = moderate (40-80%), L = low (<40%).

Species	Young		Mature		Old		Age			Year	
	mean $\pm$ SD range		mean $\pm$ SD range		mean $\pm$ SD range		F (df=2,6)	P	Power	F (df=1,6)	P
Ruffed Grouse	0.15 $\pm$ 0.13 0.00 - 0.24		0.02 $\pm$ 0.03 0.00 - 0.06		0.00 $\pm$ 0.00		3.37	0.105	L	2.56	0.161
Three-toed Woodpecker	0.01 $\pm$ 0.01 0.00 - 0.02		0.08 $\pm$ 0.09 0.00 - 0.18		0.29 $\pm$ 0.21 0.14 - 0.53		3.56	0.096	L	0.03	0.868
Yellow-bellied Flycatcher	0.28 $\pm$ 0.20 0.12 - 0.50		0.14 $\pm$ 0.11 0.01 - 0.22		0.03 $\pm$ 0.05 0.00 - 0.08		2.74	0.143	L	0.17 (Season)	0.693
Gray Jay	0.56 $\pm$ 0.14 0.44 - 0.71		0.48 $\pm$ 0.12 0.38 - 0.61		0.46 $\pm$ 0.11 0.33 - 0.53		0.57	0.591	H	1.70 (Season)	0.240
Boreal Chickadee	0.18 $\pm$ 0.13 0.06 - 0.31		0.18 $\pm$ 0.09 0.10 - 0.28		0.21 $\pm$ 0.06 0.15 - 0.28		0.12	0.891	L	5.71	0.054
Brown Creeper	0.00 $\pm$ 0.00		0.05 $\pm$ 0.09 0.00 - 0.15		0.19 $\pm$ 0.17 0.00 - 0.31		2.52	0.161	L	1.43	0.277
Red-breasted Nuthatch	0.03 $\pm$ 0.01 0.02 - 0.05		0.08 $\pm$ 0.06 0.03 - 0.14		0.36 $\pm$ 0.01 0.35 - 0.38		80.66 (Interaction)	0.000	H	0.79	0.407
Winter Wren	0.00 $\pm$ 0.00		0.05 $\pm$ 0.05 0.00 - 0.10		0.38 $\pm$ 0.19 0.21 - 0.58		9.59	0.014	L	0.00	1.000
Golden-crowned Kinglet	0.01 $\pm$ 0.01 0.00 - 0.02		0.54 $\pm$ 0.08 0.46 - 0.63		0.66 $\pm$ 0.08 0.57 - 0.74		75.63 (Interaction)	0.000	H	3.71 (Season)	0.103
Ruby-crowned Kinglet	0.12 $\pm$ 0.10 0.06 - 0.23		0.42 $\pm$ 0.08 0.33 - 0.50		0.36 $\pm$ 0.31 0.10 - 0.69		2.12 (Interaction)	0.201	L	6.93	0.039
Swainson's Thrush	0.94 $\pm$ 0.56 0.44 - 1.54		0.69 $\pm$ 0.48 0.15 - 1.06		0.36 $\pm$ 0.31 0.14 - 0.71		1.20	0.363	L	0.19 (Season)	0.679
Hermit Thrush	0.22 $\pm$ 0.21 0.00 - 0.43		0.02 $\pm$ 0.02 0.00 - 0.04		0.00 $\pm$ 0.00		2.81	0.138	L	1.86	0.222

Species	Young		Mature		Old		Age			Year	
	mean $\pm$ SD range		mean $\pm$ SD range		mean $\pm$ SD range		F (df=2,6)	P	Power	F (df=1,6)	P
Varied Thrush	0.07 $\pm$ 0.04 0.02 - 0.10		0.24 $\pm$ 0.08 0.15 - 0.32		0.21 $\pm$ 0.08 0.13 - 0.29		4.90	0.055	M	0.07	0.802
American Robin	0.22 $\pm$ 0.17 0.02 - 0.33		0.07 $\pm$ 0.06 0.00 - 0.11		0.00 $\pm$ 0.00		3.32	0.107	L	2.42	0.170
Warbling Vireo	0.88 $\pm$ 0.58 0.23 - 1.31		0.03 $\pm$ 0.01 0.01 - 0.04		0.02 $\pm$ 0.04 0.00 - 0.07		6.64	0.030	L	0.04	0.842 (Season)
Tennessee Warbler	0.10 $\pm$ 0.15 0.00 - 0.28		0.03 $\pm$ 0.03 0.00 - 0.06		0.01 $\pm$ 0.02 0.00 - 0.03		0.85	0.474	L	0.11	0.750
Orange-crowned Warbler	0.85 $\pm$ 0.32 0.52 - 1.17		0.02 $\pm$ 0.03 0.00 - 0.06		0.01 $\pm$ 0.02 0.00 - 0.04		19.59	0.002	L	9.98	0.019
Yellow-rumped Warbler	1.67 $\pm$ 0.23 1.42 - 1.88		1.76 $\pm$ 0.38 1.42 - 2.17		1.47 $\pm$ 0.26 1.29 - 1.76		0.76	0.508	H	2.98	0.135
Wilson's Warbler	0.28 $\pm$ 0.23 0.02 - 0.47		0.16 $\pm$ 0.24 0.01 - 0.43		0.16 $\pm$ 0.12 0.03 - 0.26		0.33	0.730	L	4.06	0.091 (Season)
Chipping Sparrow	0.73 $\pm$ 0.11 0.61 - 0.81		0.47 $\pm$ 0.37 0.22 - 0.89		0.37 $\pm$ 0.10 0.26 - 0.44		2.00	0.216	L	5.07	0.065
Dark-eyed Junco	1.22 $\pm$ 0.37 0.94 - 1.65		0.74 $\pm$ 0.24 0.53 - 1.00		0.98 $\pm$ 0.31 0.72 - 1.32		1.78	0.247	M	0.91	0.377
White-throated Sparrow	0.24 $\pm$ 0.15 0.06 - 0.33		0.01 $\pm$ 0.01 0.00 - 0.01		0.01 $\pm$ 0.02 0.00 - 0.03		6.85	0.028	L	1.91	0.216
Lincoln's Sparrow	0.11 $\pm$ 0.01 0.10 - 0.12		0.03 $\pm$ 0.04 0.00 - 0.07		0.03 $\pm$ 0.04 0.00 - 0.07		7.62	0.023	L	0.66	0.449
White-winged Crossbill	0.00 $\pm$ 0.00		0.24 $\pm$ 0.17 0.04 - 0.36		0.32 $\pm$ 0.13 0.21 - 0.46		5.54 (Interaction)	0.043	L	1.38	0.284 (Season)
Pine Grosbeak	0.04 $\pm$ 0.06 0.00 - 0.10		0.04 $\pm$ 0.02 0.01 - 0.06		0.11 $\pm$ 0.05 0.06 - 0.14		2.66 (Interaction)	0.149	L	0.31	0.598

Table 2.5. Number of birds observed, by migratory pattern, foraging mode, and nest location, in three age classes of forest in west-central Alberta. Units are number of observations / plot / visit. $n = 3$ sites per age class. Age and Year are from repeated measures ANOVA, with mean number of observations in 3 sessions (May/July 1991, June 1991, June 1992) as the repeated measure. Year = result of contrast between June 1991 and June 1992 (session effect not shown). (Interaction) = significant ($p < 0.05$) interaction between age and session terms. (Season) = significant ($p < 0.05$) contrast between May/July 1991 and June 1991. Power = minimum probability of rejecting the null hypothesis of no difference among age classes if $p = 0.05$ and age classes differed by 50% above and below the overall mean. H = high (>80%), M = moderate (40-80%), L = low (<40%).

	Young mean $\pm$ SD range	Mature mean $\pm$ SD range	Old mean $\pm$ SD range	Age			Year	
				F (df=2,6)	P	Power + 50%	F (df=1,6)	P
Migratory pattern								
Permanent resident	1.00 $\pm$ 0.16 0.83 - 1.15	1.21 $\pm$ 0.22 0.96 - 1.36	2.01 $\pm$ 0.28 1.76 - 2.31	17.01	0.003	H	0.35	0.578
Short distance migrant	5.51 $\pm$ 0.61 5.03 - 6.19	4.37 $\pm$ 1.21 3.67 - 5.76	4.46 $\pm$ 0.81 3.97 - 5.40	1.45	0.306	H	0.23	0.647
Long distance migrant	2.76 $\pm$ 0.40 2.50 - 3.22	1.10 $\pm$ 0.79 0.28 - 1.85	0.63 $\pm$ 0.48 0.17 - 1.13	11.07 (Interaction)	0.010	M	0.01	0.915
Foraging mode								
Ground glean	3.05 $\pm$ 0.33 2.83 - 3.43	1.67 $\pm$ 0.70 1.17 - 2.47	2.01 $\pm$ 0.17 1.89 - 2.21	7.38	0.024	H	0.33	0.589
Foliage glean	5.70 $\pm$ 0.40 5.25 - 6.00	4.63 $\pm$ 1.41 3.54 - 6.22	4.22 $\pm$ 1.28 3.39 - 5.69	1.39 (Interaction)	0.318	H	0.00 (Season)	0.991
Bark glean / excavate	0.04 $\pm$ 0.03 0.02 - 0.07	0.22 $\pm$ 0.17 0.03 - 0.32	0.84 $\pm$ 0.36 0.49 - 1.21	10.10	0.012	L	0.53	0.494
Aerial insectivore	0.48 $\pm$ 0.38 0.25 - 0.92	0.16 $\pm$ 0.09 0.06 - 0.22	0.03 $\pm$ 0.05 0.00 - 0.08	3.08	0.120	L	0.06 (Season)	0.808

	Young	Mature	Old	Age			Year	
	mean $\pm$ SD range	mean $\pm$ SD range	mean $\pm$ SD range	F (df=2,6)	P	Power + 50%	F (df=1,6)	P
Nest location								
Ground	3.46 $\pm$ 0.53 2.90 - 3.94	1.24 $\pm$ 0.56 0.85 - 1.88	1.61 $\pm$ 0.25 1.42 - 1.89	19.66	0.002	H	1.03	0.349
Shrubs or trees	2.01 $\pm$ 0.39 1.64 - 2.42	1.24 $\pm$ 0.79 0.49 - 2.06	0.73 $\pm$ 0.36 0.40 - 1.11	4.16	0.074	M	0.52 (Season)	0.496
Coniferous trees	2.49 $\pm$ 0.46 2.03 - 2.94	3.73 $\pm$ 0.79 3.15 - 4.63	3.63 $\pm$ 0.82 3.15 - 4.57	2.86	0.134	H	1.34	0.291
Deciduous trees	0.96 $\pm$ 0.63 0.23 - 1.36	0.03 $\pm$ 0.01 0.01 - 0.04	0.02 $\pm$ 0.04 0.00 - 0.07	6.51	0.031	L	0.00 (Season)	0.951
Conif. / Decid. trees	0.05 $\pm$ 0.04 0.02 - 0.10	0.02 $\pm$ 0.03 0.00 - 0.06	0.03 $\pm$ 0.02 0.00 - 0.04	0.62	0.570	L	0.03	0.875
Tree cavity	0.33 $\pm$ 0.15 0.17 - 0.46	0.44 $\pm$ 0.08 0.35 - 0.49	1.10 $\pm$ 0.31 0.79 - 1.40	12.78	0.007	M	1.02 (Season)	0.353

Table 2.6. Factor loadings of 3 principal components from a PCA of habitat attributes of 93 forested plots west-central Alberta. Factor loadings of less than | 0.10 | are not shown.

	PC 1	PC 2	PC 3
Eigenvalue	4.43	3.56	2.53
Variance explained	25%	20%	14%
Habitat attribute	Factor loading		
Short deciduous understorey	0.86		
Tall deciduous understorey	0.86		-0.21
Short coniferous understorey	-0.72	-0.12	-0.26
Shrub height	0.68		-0.20
% Subalpine fir	-0.67		-0.53
Shrub canopy closure	0.66		-0.16
% Pine	0.62	-0.26	
# Small live trees	-0.15	-0.86	
Tree height		0.85	0.42
% White spruce		0.73	-0.22
# Large live trees	-0.13	0.73	
Tall coniferous understorey	-0.37	-0.66	-0.16
# Medium & large dead trees	-0.34	0.51	
# Medium live trees			0.72
% Black spruce		-0.47	0.71
# Small dead trees	-0.16		0.70
% Deciduous trees	0.33	-0.27	-0.44
Tree canopy closure	-0.22	0.28	0.42

Table 2.7. Factor loadings of 3 principal components from a PCA of weighted habitat attributes for 25 bird species in west-central Alberta. Factor loadings of less than | 0.10 | are not shown.

	PC 1	PC 2	PC 3
Eigenvalue	10.94	2.61	2.06
Variance explained	61%	15%	11%

Habitat attribute	Factor loading		
Shrub height	-0.93	-0.21	
Tall deciduous understorey	-0.93	-0.28	-0.14
% Pine	-0.84	-0.30	
Short deciduous understorey	-0.83	-0.51	
Shrub canopy closure	-0.82		-0.27
Short coniferous understorey	0.77	0.39	-0.25
# Small dead trees	0.63	0.55	0.30
% Deciduous trees	-0.58	-0.52	-0.52
# Small live trees		-0.97	
# Large live trees	0.44	0.87	
Tall coniferous understorey		-0.83	
Tree height	0.52	0.80	0.27
% White spruce	0.43	0.79	0.17
# Medium & large dead trees	0.55	0.75	-0.14
Tree canopy closure	0.49	0.71	0.12
% Subalpine fir	0.24	-0.19	-0.91
% Black spruce	0.36	-0.25	0.85
# Medium live trees	0.60	0.40	0.61

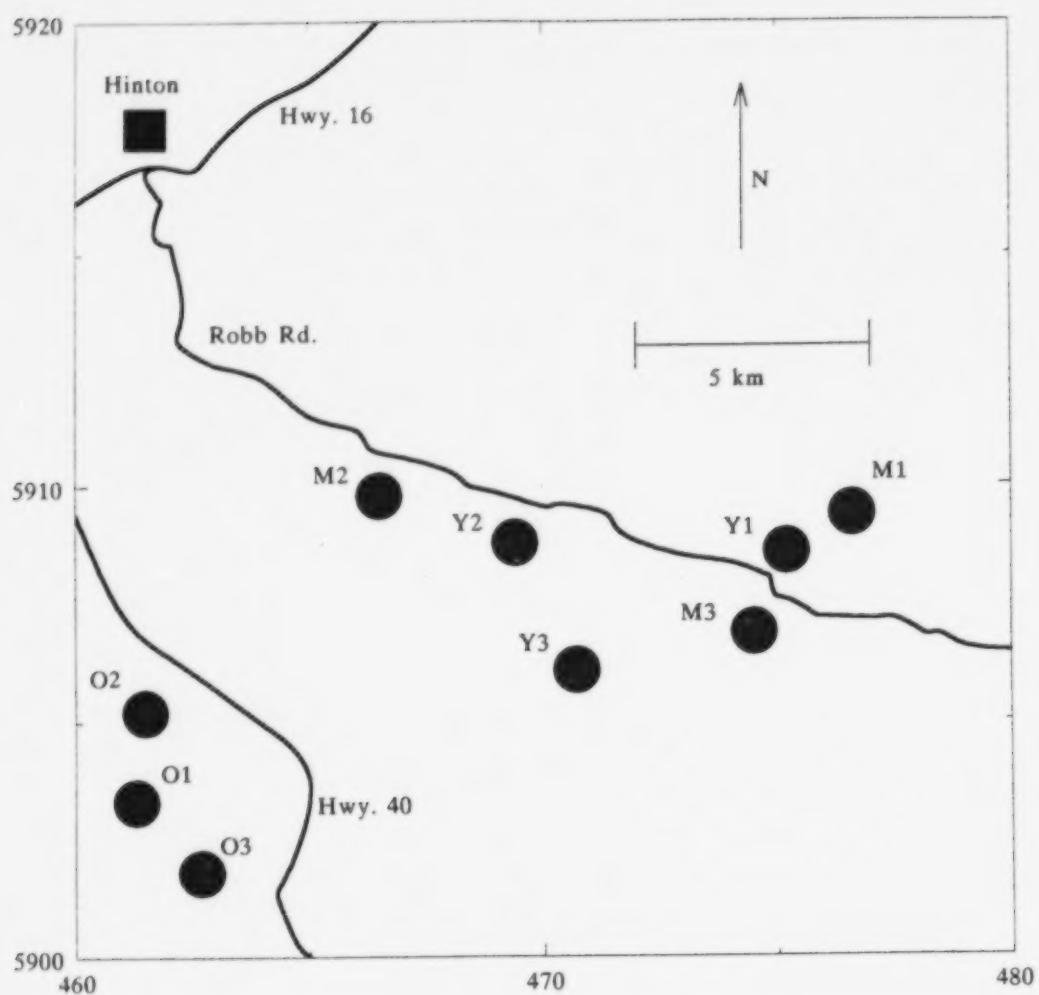
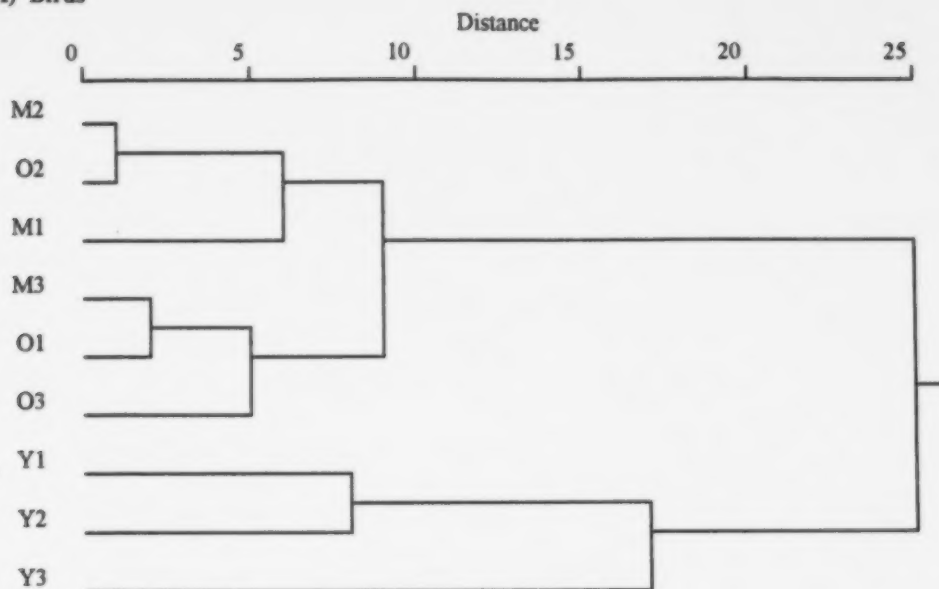


Figure 2.1. Map of the study area indicating study site locations. Axis labels are UTM references.
Y = young, M = mature, O = old.

A) Birds



B) Habitat

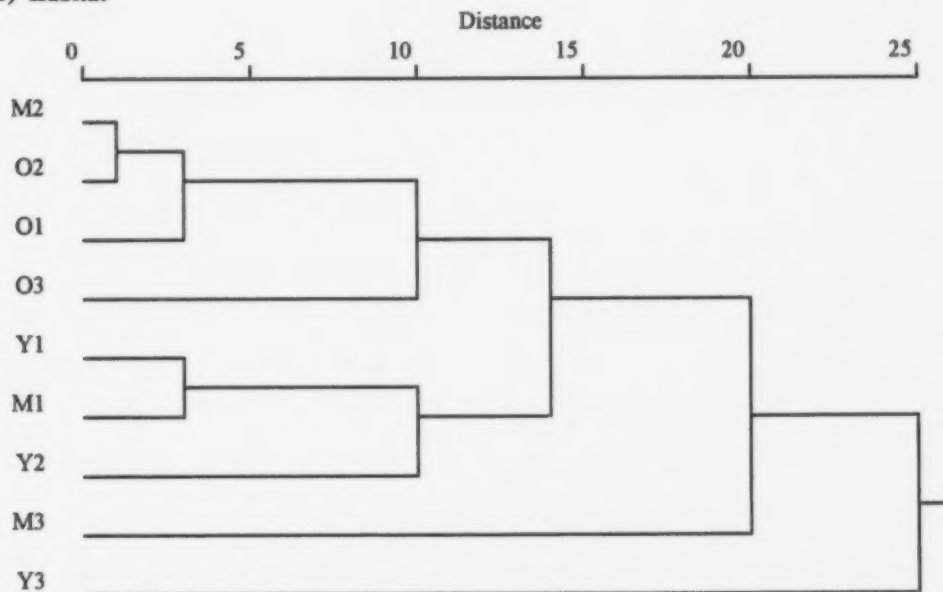


Figure 2.2. Patterns of similarity among 9 forested sites in west-central Alberta based on cluster analysis of A) counts of birds in each site, and B) mean habitat attributes of each site. Distance = chi-square measure of dissimilarity (A) and squared euclidean distance (B), both scaled to a maximum of 25. Y = young, M = mature, O = old.

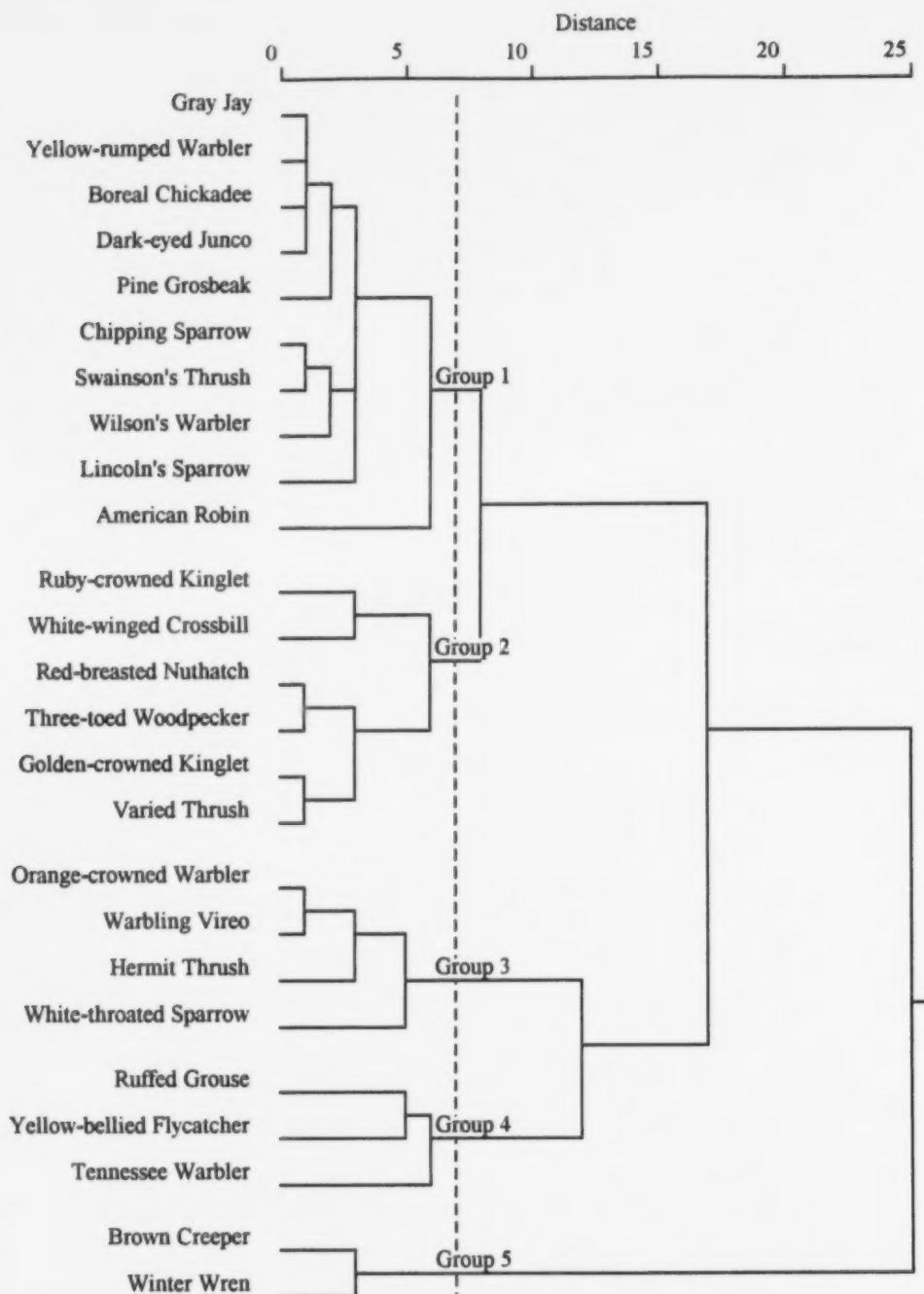


Figure 2.3. Patterns of similarity among 25 bird species in west-central Alberta, based on a cluster analysis of weighted mean habitat attributes measured in 12-93 plots per species. Distance = squared euclidean distance, scaled to a maximum of 25. Vertical dashed line is arbitrarily drawn to illustrate 5 groups discussed in the text.

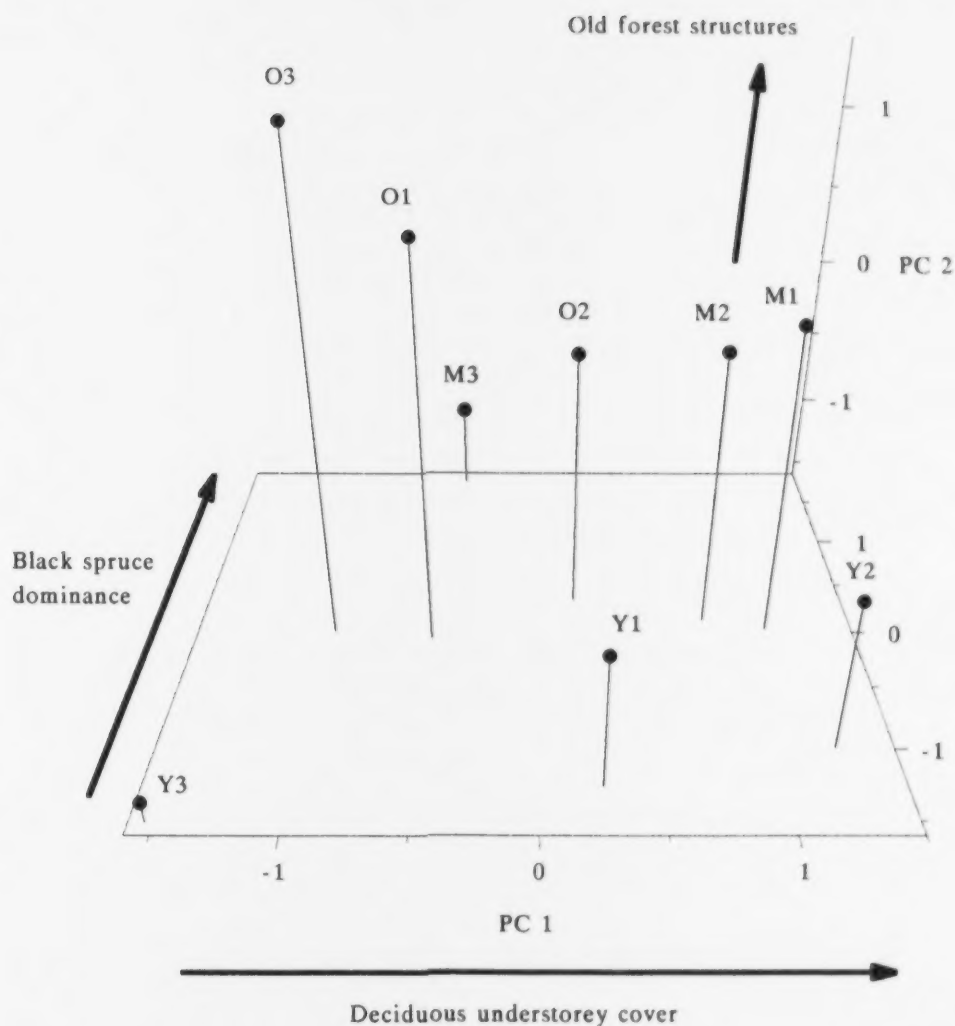


Figure 2.4. Mean principal component scores for each study site, from a PCA of habitat attributes (Table 2.6). Axis labels were interpreted from factor loadings (Table 2.6); arrows point towards high values. Axis lengths are proportional to the variance explained by each principal component. Y = young, M = mature, O = old.

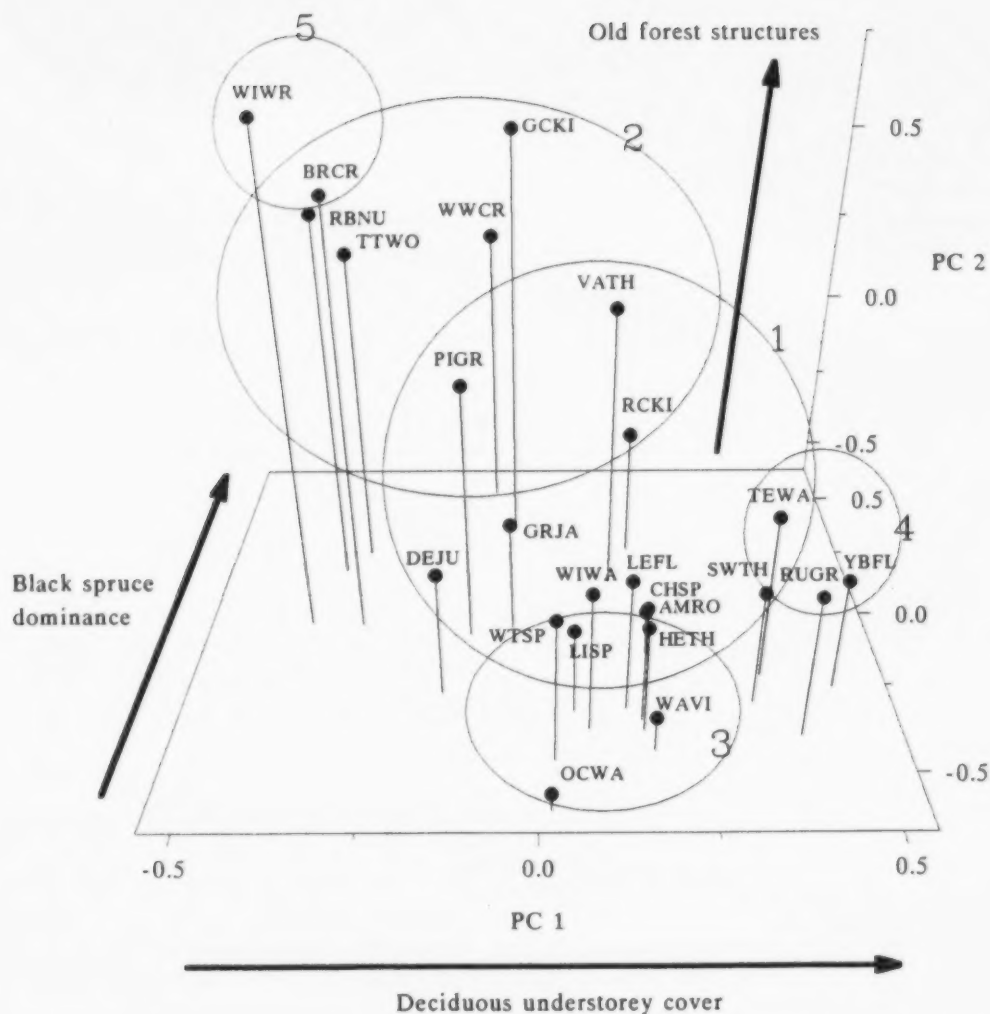


Figure 2.5. Correlations between bird abundance and 3 principal components from a PCA of habitat attributes (Table 2.6). Axis labels were interpreted from factor loadings; arrows point towards high values. Axis lengths are proportional to the proportion of variance explained by each principal component. Only species whose abundance was significantly ($p < 0.05$) correlated with at least one PC are shown; species codes in Appendix 1. Numbers 1-5 and corresponding ellipses refer to species groups described in the text.

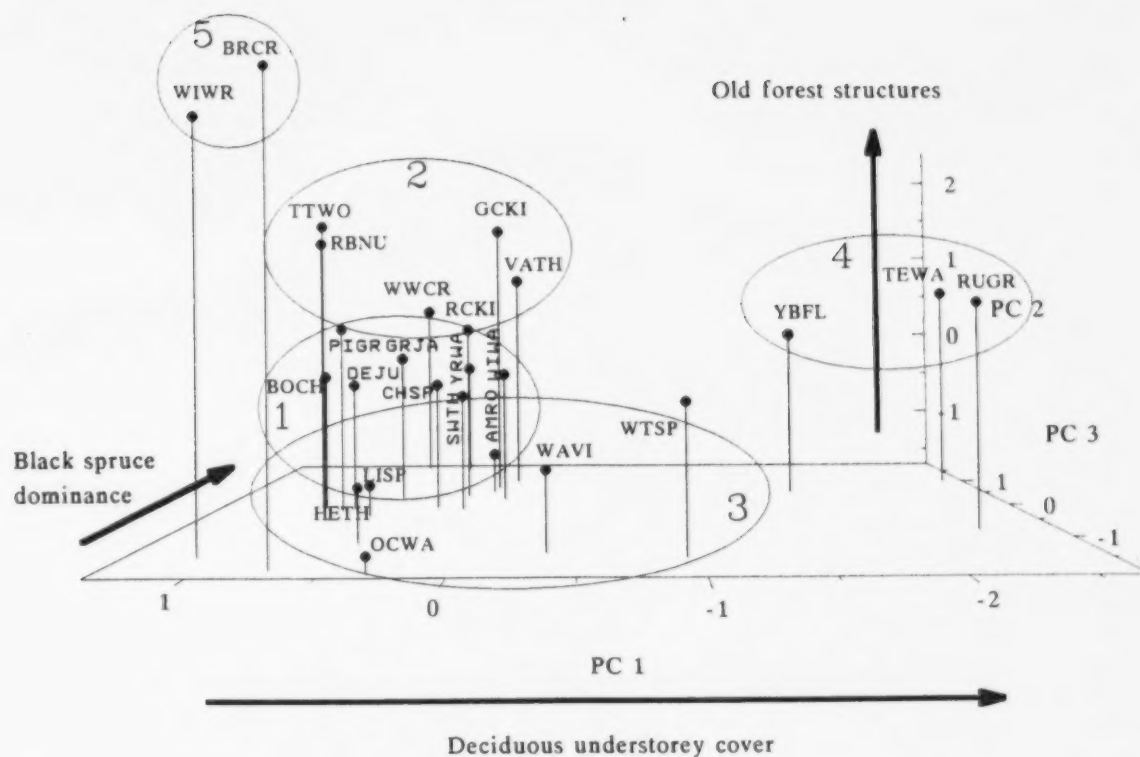


Figure 2.6. Principal component scores for bird species, from a PCA of weighted mean habitat attributes (Table 2.7). Axis labels were interpreted from factor loadings; arrows point towards high values. Axis lengths are proportional to the proportion of variance explained by each principal component. Species codes in Appendix 1. Numbers 1-5 and corresponding ellipses refer to species groups described in the text.

3 Preliminary tests of habitat suitability models for Varied Thrush, Ovenbird and Red Squirrel

3.1 Introduction

Approaches and technologies that facilitate the production of wood fibre in forest ecosystems are more advanced than those for management of other forest values such as animal populations and their habitats. To address this imbalance, managers in west-central Alberta are developing an approach to integrating timber and wildlife management in an industrially managed forest using habitat suitability index (HSI) models (USDI 1981) for selected vertebrate species (Bonar *et al.* 1990). The 30 species initially chosen for model development include species that are economically or socially important in the region (*e.g.*, ungulates), rare species, and 16 indicator species selected to represent a range of habitat types in the region (Bonar *et al.* 1990). The current and future habitat supply for each of the modelled species are to be predicted by linking each HSI model with existing timber supply models (Walker 1990) developed for west-central Alberta. These predictions would then be available to managers attempting to balance future requirements for wood fibre and wildlife habitat. The 16 indicator species provide a mechanism for predicting the future supply of a range of habitat types under a variety of forest management scenarios, which could facilitate the conservation of habitat diversity in the region (Bonar *et al.* 1990).

HSI models for 5 of these 30 species were developed and proposed in 1990 (Bonar *et al.* 1990). These species are Hoary Bat (*Lasiurus cinereus*), Red Squirrel (*Tamiasciurus hudsonicus*), Ovenbird (*Seiurus aurocapillus*), Varied Thrush (*Ixoreus naevius*) and Savannah Sparrow (*Passerculus sandwichensis*). The models were based on literature reviews of habitat requirements (Quinlan *et al.* 1990), and their development followed the standards proposed by the U.S. Fish and Wildlife Service (USDI 1980, 1981). Each model consists of predicted relationships between habitat suitability and one or more habitat variables, with habitat suitability interpreted as the capacity of a particular habitat to support a given species (USDI 1981, Schamberger and O'Neil 1986). The predicted relationships are combined using functions that reflect the relative importance of each variable to overall habitat suitability.

The objective of this study was to test the ability of 3 HSI models (Varied Thrush, Ovenbird, Red Squirrel) to accurately predict population density as estimated from point samples (Reynolds *et al.* 1981). Because density is not always directly correlated with habitat quality (Van Horne 1983), these tests are preliminary, and are best viewed as a part of model development and refinement (Marcot *et al.* 1983). More complete tests are required to assess model validity according to a range of criteria, including generality, realism, resolution, accuracy, precision and many others (Marcot *et al.* 1983, Bunnell 1989, Morrison *et al.* 1992). In this study, I tested the hypothesis that for each HSI model, abundance estimated from point samples was directly proportional to predicted habitat suitability. Revised versions of each model are proposed based on the results of these tests, as are summaries of field data for 12 additional species of birds for which HSI models may be developed in the future (R. Bonar, pers. comm).

3.2 Study area

The HSI models are to be applied to lands within the Forest Management Agreement (FMA) area near Hinton, Alberta (53°25'N, 117°35'W) licensed to Weldwood of Canada Ltd. (Bonar *et al.* 1990), and locations sampled in this study were within or adjacent to the FMA area. Much of the region is dissected by foothills oriented northwest to southeast, with elevation rising from less than

900 m in the northeast to over 1600 m near the Front Ranges of the Rocky Mountains (Corns and Annas 1986). Forest cover is strongly correlated with elevation, and the region includes 3 Forest Sections as defined by Rowe (1972): (Boreal) Lower Foothills, (Boreal) Upper Foothills and (Subalpine) East Slope Rockies. Mature forest in the latter 2 sections is dominated by lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), or black spruce (*P. mariana*), with deciduous trees (mainly aspen, *Populus tremuloides*) dominant only in parts of the Lower Foothills and at lower elevations further west within the Athabasca River valley. Other major rivers in the area include the Berland, McLeod, and Embarrass.

3.3 Methods

3.3.1 Site selection

I sampled birds, squirrels, and habitat attributes at 147 sites (Fig. 3.1), which were dominated either by forest that had not previously been logged, or by forest that had been logged by clearcutting since 1956. Sites were selected subjectively, based on accessibility, the availability of forest inventory information, but were intended to represent a wide range of forest types in the region. Data from 4 groups of sites were combined in order to assess habitat relationships, and although sampling protocols differed somewhat among groups, I considered the estimates of animal abundance and habitat attributes to be comparable. The first group (group 1) included 72 sites, each comprised of 10 sample plots whose centres were 400 m apart. The second group (group 2) included 9 sites, each containing 12 sample plots 300 m apart. Bird populations in this group were described in Chapter 2. The third group (group 3) included 17 sites, all of which contained 5 plots 300 m apart, except for 2 sites containing one plot each and a third containing 6 plots. The fourth group (group 4) included 49 sites, each containing an average of 5 plots (range 1-12) approximately 300 m apart. In logged sites, plots in which residual patches of unlogged forest occurred within 150 m of the plot centre (125 plots) were excluded from all analyses. A total of 1,044 sample plots (648 unlogged, 396 logged) were included in analyses.

3.3.2 Bird and squirrel sampling

I sampled birds and squirrels using point samples (Reynolds *et al.* 1980) in June of 1992 (groups 1 and 2), and between late May and early July of 1990 (groups 3 and 4). Sampling was conducted on days with little or no rain and winds less than 20 km/h, usually beginning one half-hour before local sunrise (approximately 0500 MST in June), and ending within 4 hours. At each plot, a single observer counted all birds and squirrels observed (*i.e.*, seen or heard) from the plot centre within a 10 minute period; one or two sites were visited per day. The observer also estimated the distance to each animal when first observed, and those judged to be more than 150 m away were excluded from analyses. Including more distant observations (*i.e.*, increasing plot size) would increase within-plot habitat heterogeneity, possibly obscuring habitat relationships, while reducing plot size would reduce the number of plots in which a species was counted; the 150 m radius was a compromise between these two factors. In group 1, 6 observers sampled 12 sites once each, with sites distributed evenly among observers based on preliminary assessments of dominant forest cover. A seventh observer sampled all group 2 sites twice. The sites in group 3 were sampled between 1 and 4 times by two observers, and the sites in group 4 were sampled once, also by two observers. I estimated animal abundance in each plot by calculating the mean number of observations of each species per 10 minute sample period (*i.e.*, total count standardized by sampling effort).

3.3.3 Habitat sampling

In each plot, I obtained estimates of habitat variables that were included in the 3 proposed HSI models, or could potentially be added to revised models. For sites in groups 1 and 2 ($n=703$ plots), habitat assessments were obtained for an area of 7.1 ha (150 m radius circle) around the plot centre. Because this plot area frequently contained more than one cutblock or cover type polygon, most values used in analyses were the mean of all cutblocks or polygons weighted by the relative area of each cutblock or polygon in the plot (see exceptions, below). For sites in group 3 ($n=78$ plots), habitat assessments were obtained only at the centre of each plot. Plots in group 4 usually were located within a single cutblock or cover type polygon, and only two variables, stand age (223 plots), and elevation (263 plots) were available.

Stand age in unlogged forest was obtained from forest cover inventories derived from a fire history study conducted by Northwestern Pulp and Power Ltd. (Weldwood of Canada Ltd. files). In logged forest, the year of harvesting was determined from company silvicultural history files (396 plots). Most plots in logged forest contained cutblocks harvested in both first and second passes, with 10-20 years between passes.

Tree height in unlogged forest was obtained from digital forest cover inventories (420 plots in group 1) or was measured directly using a Sunto clinometer (133 plots in groups 2, 3). In logged forest, tree height was estimated on the ground during field checks. In all plots, tree height was the height of dominant and codominant trees in the stand (Alberta Forestry, Lands and Wildlife 1991).

Tree crown closure in unlogged forest was obtained from digital forest cover inventories (420 plots in group 1), or was estimated on the ground during field checks (133 plots in groups 2, 3). In logged forest, crown closure was estimated on the ground during field checks. In all plots, crown closure was defined as the percent of ground covered by a vertical projection of dominant and codominant tree crowns, in 4 density classes (Alberta Forestry, Lands and Wildlife 1991). I used the mid-point of each density class in calculations of area-weighted means for each plot.

Density of standing dead trees in group 1 (610 plots) was obtained by counting the number of standing dead trees over 15 cm diameter at breast height and over 2 m tall, within a 100 m x 20 m belt transect through the plot centre. In group 2 (95 plots), such trees were counted in 10 x 10 m plots in each cutblock or cover type polygon within 150 m of the plot centre, and in group 3 (78 plots), such trees were counted within a 11.3 m radius circle around the plot centre.

Shrub height was estimated to the nearest metre using the design described for standing dead trees, except for logged sites in group 1 (190 plots), in which estimates of shrub height for each cutblock were used to calculate area-weighted means.

Shrub crown closure was estimated to the nearest 10% using the design described for shrub height.

Tree species composition, or the contribution of each tree species to crown closure (defined above), was estimated to the nearest 10% (Alberta Forestry, Lands and Wildlife 1991) during field checks. Estimates were made using the design described for shrub height.

Site index, or the estimated height of dominant and codominant trees at 50 years of age, was obtained in unlogged forest only, for all sites in group 1 (420 plots) and one site in group 2 (12 plots), from digital forest inventories.

Elevation at the centre of all plots was obtained from 1:50,000 scale topographic maps.

3.3.4 HSI model testing and revision

In order to illustrate patterns of abundance along habitat gradients within logged and unlogged forest, I divided each habitat variable into several categories, attempting to distribute sample sizes across habitat gradients. I excluded categories with fewer than 10 plots to avoid excessive sampling bias (e.g., all plots in a category sampled by the same observer). I then calculated the mean number of animals observed per 10 minute sample period in each category. I re-expressed these means as the proportion of maximum abundance, and plotted them against the midpoint of each habitat category. Sample sizes for each habitat category are given in Fig. 3.2. The same procedure was followed to express the correlations among habitat variables by replacing the number of animals observed in a plot with the corresponding value of a selected habitat variable. Correlations with other habitat variables are given for elevation (Fig. 3.3), stand age (Fig. 3.4) and proportion of deciduous trees (Fig. 3.5).

The original HSI models for each of the 3 species (Bonar *et al.* 1990) are given in Table 3.1, with the originally proposed suitability index relationships given in Figs. 3.6 (Varied Thrush), 3.7 (Ovenbird) and 3.8 (Red Squirrel). For each of these 3 species, I calculated the HSI value of each plot, using the variables included in the HSI model. I then determined the mean number of animals observed per 10 minute sample period in 5 categories of HSI values (0-0.2, 0.2-0.4, 0.4-0.6, 0.6-0.8 and 0.8-1.0). Categories with fewer than 10 plots were excluded. I re-expressed these means as the proportion of maximum abundance, and plotted them against the midpoint of each HSI category.

I assessed the overall performance of each model by calculating the absolute value of the residuals of the relationship between observed abundance in an HSI category, and that expected if abundance was directly proportional to habitat suitability (USDI 1990). The means of these residuals provided indices of overall model performance, with 0 indicating a perfect fit between observed and predicted abundance, and larger numbers indicating poorer model performance. This index is particularly sensitive to deviations at both extremes of the HSI scale (*i.e.*, low and high HSI values).

For each model, proposed revisions were based on visual comparison of the original model's suitability relationships and the observed patterns of abundance. I also applied alternative functions (USDI 1981) to combine model variables. I followed an iterative process for each model, evaluating overall model output and performance measure after each modification to a suitability relationship or function. The final choice of revision was based on an improved correlation between observed abundance in an HSI category and that expected if abundance was directly proportional to habitat suitability (see above).

3.4 Results

3.4.1 Varied Thrush

As was suggested by the original HSI model, very few Varied Thrushes were observed in logged stands, all of which were younger than the minimum 50 years proposed by the model (Fig. 3.6). (The following results therefore refer to unlogged forest only). The abundance data for unlogged forest suggested an association with older stands having a low site index, dominated by spruce and fir (black spruce in particular) and an association with sites having an open shrub understorey dominated by low shrubs (Fig. 3.6). Of the 3 variables comprising the original HSI model (Table 3.1), the correlation between proposed suitability and abundance in unlogged forest appeared to be reasonably good for stand age and percent spruce and fir (Fig. 3.6). However, abundance was considerably greater in plots with relatively low tree crown closure than suggested by

the model (Fig. 3.6). The additional discrepancy for plots with dense tree canopy closure (Fig. 3.6) may have been influenced by small sample size of plots with dense tree canopy closure (Fig. 3.2).

The correlation between abundance in each HSI category and that expected if abundance was directly proportional to habitat suitability was relatively good, with abundance tending to increase with increasing HSI values (Fig. 3.6). However, abundance was consistently moderate (30% of maximum) in plots that had a range HSI values (0.1 through 0.5). This resulted in an overall model performance that was only fair (0.34, Table 3.1).

Revisions to proposed suitability relationships to better reflect the patterns suggested by abundance data included: shifting the minimum tree crown closure down to 30% from 50%; shifting the minimum proportion of spruce and fir down to 10% from 25%; and shifting the age at which stands become highly suitable to 120 years from 90 years (Fig. 3.9). The function used to combine habitat variables, which was based on the assumption that tree crown closure and species composition were more important than stand age (Bonar *et al.* 1990) was changed to a simple multiplicative function in which all variable receive equal weighting (Table 3.1). These revisions improved overall model performance in unlogged forest by reducing mean residuals from 0.34 to 0.09 (Table 3.1, Fig. 3.9).

3.4.2 Ovenbird

Very few Ovenbirds were observed in logged stands (Fig. 3.7), and the following results therefore refer only to unlogged forest. The abundance data in unlogged forest suggested a positive association with stands having a relatively tall, dense overstorey dominated by deciduous trees, and an affinity to sites with a closed shrub understorey dominated by tall shrubs (Fig. 3.7). For each of the 3 variables comprising the original HSI model (tree canopy closure, percent deciduous trees, stand age; Table 3.1), the correlation between proposed suitability and abundance in unlogged forest appeared to be reasonably good (Fig. 3.7).

However, the correlation between abundance in each HSI category and that expected if abundance was directly proportional to habitat suitability was very poor, with no plots achieving an HSI value of greater than 0.0-0.2 (Fig. 3.7). This resulted in very poor overall model performance (0.89, Table 3.1).

The poor performance of the original HSI model appeared to be caused primarily by the predicted decline in habitat suitability of stands older than 60 years. Although this trend was apparently supported by abundance data (Fig. 3.7) it may have been an artifact of the strong association of this species with deciduous trees (Fig. 3.7), which were less dominant in the older stands sampled (Fig. 3.5). Maintaining high suitability values in all stands older than 60 years improved overall model performance in unlogged forest considerably, reducing mean residuals from 0.89 to 0.08 (Table 3.1, Fig. 3.9). Changes to the function used to combine habitat variables (Table 3.1) did not provide any additional improvement in performance.

3.4.3 Red Squirrel

Red squirrels were observed in both unlogged and logged forest, but were consistently more common in unlogged stands (Fig. 3.8). Highest abundance was in coniferous stands dominated by white spruce or white spruce and fir, but abundance tended to decline at higher elevations (Fig. 3.8). Older, taller stands appeared to be preferred over younger, shorter stands, and there was an apparent avoidance of stands dominated by deciduous trees. Of the 4 variables comprising the original HSI model (Table 3.1), the correlation between proposed suitability and abundance appeared to be

reasonably good for tree canopy closure; the discrepancy for plots with dense tree canopy closure may have been influenced by small sample size (Fig. 3.2). The correlations with proposed suitability for both percent of coniferous trees and percent of spruce were fair, although the relationship between abundance and percent spruce appeared to differ between logged and unlogged forest (Fig. 3.8).

The correlation between abundance in each HSI category and that expected if abundance was directly proportional to habitat suitability was excellent for logged forest (mean residuals of 0.06), and modest for unlogged forest (mean residuals of 0.20; Table 3.1, Fig. 3.8). However, no plots in unlogged forest were given an HSI value of less than 0.4-0.6, and abundance in the upper 3 HSI categories did not increase linearly (Fig. 3.8).

Revisions to the proposed suitability relationships were limited to shifting the age at which stands become highly suitable to 120 years from 40 years (Fig. 3.9). In addition, the function used to combine habitat variables in the original model (Table 3.1) made it possible for HSI values to exceed 1.0 (e.g., if all habitat variables were optimal), an undesirable condition (USDI 1981). The revised function in Table 3.1 corrects this condition, but additional changes to the function did not provide any additional improvement in performance. The revised model performed better in unlogged forest by reducing mean residuals from 0.20 to 0.14 (Table 3.1, Fig. 3.9).

3.5 Discussion

3.5.1 HSI model assumptions

A central assumption of all HSI models is that the included habitat variables are directly related to population limitation, or that they are correlated with other factors that are so related (Van Horne and Wiens 1991). A related assumption is that the role of limiting factors does not change in different parts of the area in which the model is to be applied. For example, food availability may be limited by the proportion of a particular tree species at low elevations, but limited by the abundance of a shrub species at higher elevations. Intraspecific shifts in diet and foraging behaviour of forest birds have been documented among forest regions (Nilsson and Alerstam 1976, Rabenold 1978), and among forest types within a region (Franzreb 1983). If such shifts occur within a model's applicable area, then model predictions of habitat suitability may not be consistently correlated with important limiting factors, or with abundance as estimated in this study.

Some HSI models explicitly assume relationships exist between a model variable and another variable not included in the model. For example, the Ovenbird model assumed that closed canopy stands dominated by deciduous trees have a sparse understorey (Bonar *et al.* 1990), a potentially important relationship because Ovenbirds apparently avoid areas with dense understorey (Erskine 1977). (Note that this relationship was not supported by the data from this study; Fig. 3.7). In the red squirrel model, conifer cones were identified as a major food resource, and the model assumed that a tree's cone production begins at 15 years of age, reaching maximum production by 40 years (Bonar *et al.* 1990). The availability of conifer cones is represented by the age, proportion, and density of coniferous trees in the canopy (Bonar *et al.* 1990).

Finally, the Varied Thrush and Ovenbird models assume that stands smaller than 2 hectares and 6 hectares, respectively, are unsuitable (Bonar *et al.* 1990). However, these models and the red squirrel model assume that habitat suitability is not related to the shape of a particular habitat patch, nor to the composition and structure of adjacent habitat patches (Bonar *et al.* 1990, Van Horne and Wiens 1991). Many studies have supported alternative scenarios, in which abundance or reproductive success depends on patch size (Galli *et al.* 1976, Urban and Shugart 1986, Wenny *et al.*

1993), the prevalence of habitat edges (a function of both size and shape) (Temple and Carey 1988, Rudnicki and Hunter 1993), and the nature of the surrounding habitat matrix (Wiens *et al.* 1985). If these factors affect habitat suitability, then satisfactory model performance in existing unlogged forest (*e.g.*, Varied Thrush, Fig. 3.9) may not hold in maturing logged forest, which contains more abrupt habitat edges (*pers. obs.*).

3.5.2 Sources of variation between observed and predicted HSI values

3.5.2.1 Choice of model variables

HSI model variables were originally chosen based on an assessment of the habitat characteristics needed to meet the life requisites of food, reproduction, and cover (USDI 1981, Bonar *et al.* 1990). The two migratory bird models apply to breeding season requirements only, while the model for red squirrel applies year-round (Bonar *et al.* 1990). Variables are further limited to those that are easily measured (USDI 1981) or can be included in habitat supply models (Bonar *et al.* 1990), and sometimes a potentially important variable is replaced by a more easily measured and modelled variable (*see above*). Deleting one or more variables from a proposed HSI model would be justified if the variable was not correlated with productivity or abundance, although this seems conceptually unlikely given the probable intercorrelation of most habitat variables. Also, the strength of a variable's influence on model output depends on its proposed relationship to suitability. A variable should probably be excluded only if its inclusion in a variety of forms (suitability relationships) is repeatedly demonstrated to have little or no effect on habitat suitability. In this study, I considered the overall performance measure applied to a single sample of habitats was insufficient to justify deletions of variables from any HSI model.

Adding variables seems conceptually more reasonable than deleting them, because the abundance or productivity of animals is almost certainly affected by more than 3 or 4 variables. The plots of abundance vs. habitat variables given in Figs. 3.6 - 3.8 provide some guidance for selecting additional model variables, so long as correlations among variables (*e.g.*, Figs. 3.3 - 3.5) are considered. However, "adding a variable to a model may alter the mathematical relationships among the rest of the variables and result in an unwanted modification of the model" (USDI 1990:6-3, *pers. obs.*). In this study initial attempts to add variables quickly degenerated into "fishing expeditions" for improved correlations between abundance and HSI values that did not result in improved model performance.

Relationships between species, through predation, competition, or parasitism may also affect habitat suitability (Schamberger and O'Neil 1986). Laymon and Barrett (1986) suggested that models for some species should include a variable relating to predation, noting that low abundance could occur in habitat predicted to be optimal if the density of predators was high. For example, poor performance of an HSI model for Douglas' squirrel (*Tamiasciurus douglasii*) may have been partly due to the presence of marten (*Martes americana*) in optimal squirrel habitat (Laymon and Barrett 1986). In this study, the slightly higher abundance of red squirrels in logged forest compared to unlogged forest with a similar HSI rating (Fig. 3.8) may have been partly due to higher densities of predators (*e.g.*, marten, Northern Goshawk) in unlogged forest. If such relationships are known, then including a variable that relates to habitat suitability for predators could improve a model's performance.

3.5.2.2 Suitability relationships

Model inaccuracy may also be caused by inappropriate relationships between individual model variables and habitat suitability, and in this study suitability relationships were revised by examining the patterns in Figs. 3.6 - 3.8, considering the intercorrelations among variables illustrated in Figs. 3.3 - 3.5. The thresholds beyond which habitat becomes either unsuitable or optimal have particularly important effects (Van Horne and Wiens 1991). Also, the shape of a suitability curve may change according to the values of other variables that may or may not be included in the model. Statistical methods such as partial correlation analysis may be useful for isolating the influence of a single variable (James and McCulloch 1985), but require a more complete sample of abundance for each plot than was obtained in this study.

3.5.2.3 Model functions

There are many options for combining the effects of model variables (USDI 1981), and the choice of function can have very large effects on HSI values (Van Horne and Wiens 1991). Each of the models described in this study used compensatory relationships, in which small values for one value can be offset by large values of another variable (Table 3.1). In the two bird models, positive values for all variables are required for habitat suitability, *i.e.*, HSI equals zero when one or more variables equals zero. The red squirrel model contains a more complicated function in which positive HSI values are possible even if one or more variables equals zero (Table 3.1). A variable can also be weighted according to its proposed effect on suitability. For example, the Varied Thrush model assumed that of the 3 variables included in the model, tree canopy closure and species composition are more important than stand age (Bonar *et al.* 1990). Further analysis of the data from this study could include a sensitivity analysis of changes in the relationships among habitat variables (Van Horne and Wiens 1991) but would be *ad hoc* in nature and assume that only a small portion of the model is open to correction (Bunnell 1989). A more profitable approach would be to review and test the assumptions of resource use made during model development via carefully planned field experiments.

3.5.2.4 Point samples vs. habitat suitability

In this study, I assumed that abundance was directly related to habitat suitability, and that point samples provided accurate estimates of abundance. Neither assumption may hold for all species, or across all habitats. First, the relationship between density and habitat quality may not be linear, because of temporal population fluctuations accompanied by time lags (Van Horne 1983). Habitat generalists, and species whose high reproductive rates or dispersal abilities can temporarily saturate unsuitable habitats, may be particularly sensitive to this density/quality discrepancy (Van Horne 1983). Second, point samples are almost entirely dependent upon vocalizations (>90% of observations in this study), which may vary both diurnally and seasonally (Best 1981, Skirven 1981). In this study, I attempted to reduce the effects of seasonal and diurnal variation by ensuring that each major habitat type was sampled on a range of dates and times. Of potentially greater concern is evidence that male pairing status may influence point sampling results (Hayes *et al.* 1985, Gibbs and Wenny 1993). Unpaired males, which are probably more common in less suitable habitat, may vocalize more frequently than paired males (Gibbs and Faaborg 1989, Vickery *et al.* 1992). Point samples conducted under such conditions would not indicate that the highest abundance occurred in the most suitable habitat.

Point sample results may also differ across habitat gradients if sound transmission is affected by forest composition and structure (Richards 1981). However, variation in detectability among different forest types for most species may be minor (Finch and Reynolds 1988, Smith *et al.* 1993, Farr, unpubl. obs.) compared to other factors such as topography. For example, samples conducted from gullies probably contained fewer observations than those conducted on the side of a steep hill (pers. obs.), although topography did not appear to vary consistently among the habitats sampled in this study. Differences in the abilities of observers to detect animals (Cyr 1981) and estimate distance (Scott *et al.* 1981) may bias abundance estimates, and it was logistically difficult to ensure that each class of the 14 habitat variables was sampled equally by all observers, because detailed habitat estimates were obtained after bird sampling was completed.

Finally, incomplete sampling of habitats may cause discrepancies between assumed and actual optimal habitat (Best and Stauffer 1986). Implicit in the interpretation of HSI values (Figs. 3.6 - 3.9) is the assumption that plots with the highest HSI class represent optimal habitat (USDI 1981). This assumption may fail either because the model variables are inappropriate, or because an insufficient range of habitat conditions were sampled. Insufficient sampling of optimal habitats would result in the overestimation of expected abundance in the remaining habitats.

3.5.3 Recommendations for further research

Research to validate HSI models can occur at several levels, from i) model assumptions concerning limiting factors and the range of conditions under which assumptions are met, to ii) the choice of model variables thought to limit population viability, including their relationships to suitability and to each other, and iii) evaluating final model output and predicted habitat suitability (Chalk 1986, Schamberger and O'Neil 1986, Van Horne and Wiens 1991). Validation at the first two levels, best accomplished through controlled field experimentation or manipulative experiments (Van Horne and Wiens 1991), can provide improved understanding of model weaknesses and assumptions (Bunnell 1989), but is expensive and time-consuming (Van Horne and Wiens 1991). Validation at the third level (as in this study) allows for the earlier use of models in a planning process (Schamberger and O'Neil 1986), and is an essential part of model development (Marcot *et al.* 1983). However, satisfactory predictions obtained from one sample of habitats, without an adequate understanding of the assumptions and habitat relationships on which the model is based, may result in poor or confusing model performance in other samples (Bunnell 1989, Van Horne and Wiens 1991). Further efforts to validate HSI models in west-central Alberta should include tests of model relationships and assumptions, and the following research areas are proposed.

First, the assumption that a particular habitat variable limits productivity could be tested by monitoring reproduction and survival in carefully selected samples of habitats that differ according to one or two key variables (*e.g.*, tree crown closure and proportion of a tree species), controlling for differences in other variables as much as possible. Such studies would be appropriate for relatively common species that nest on or near the ground, such as Hermit Thrush, Ovenbird, Savannah Sparrow, Tennessee Warbler, Clay-colored Sparrow and Chipping Sparrow. Martin and Geupel (1993) provided detailed methods for locating and monitoring nests of forest birds, and Ralph *et al.* (1993) described the use of mist nets to monitor post-fledging survival. The checkerboard pattern of regenerating cutblocks common throughout this region offer excellent opportunities for "natural" experiments (James and McCulloch 1985) in which accessible, replicated, and interspersed treatments could be located in a single compartment. Repeating such a design in each of the 5 working circles would assess the degree to which relationships are consistent throughout the model's

applicable area. Comparable sampling designs in unlogged forest are more difficult to obtain, and manipulative experiments (*e.g.*, thinning, rather than clearcutting, proposed cutblocks to systematically vary canopy closure, see Szaro and Balda 1979) may be necessary.

The role of patch size, fragmentation, and landscape context in habitat suitability is another area needing further research (Verner 1986, Van Horne and Wiens 1991). In logged forest, which will eventually dominate a managed forest landscape, direct estimates of the effects of these factors, and their interactions with other model variables, is currently impossible in this region for species that do not occupy stands less than 40 years old. However, indirect estimates are possible by sampling existing isolated stands of mature unlogged forest. Most such stands are unproductive, black spruce-dominated wetlands however, and are at least 60 years older than the surrounding cutblocks. Most future regenerating tracts of mature forest will be mosaics of stands less than 20 years apart in age, a difference in habitat context that may also have large effects on habitat suitability (Wiens *et al.* 1985).

A third area of research to assist validation efforts for several species is a methodological study of the correlation between point sampling results and reproductive success. Point sampling is an efficient, relatively inexpensive way to sample bird and squirrel populations, but the actual parameter being measured is unclear (see above). Calibrating point samples using direct measures of reproductive success (*e.g.*, Vickery *et al.* 1992) in a range of habitats would assist in providing more accurate tests of HSI model assumptions and predictions.

3.5.4 HSI models and forest management

If HSI models and habitat supply analyses are capable of generating reliable predictions, then they would be useful tools to assist managers attempting to assess the effects of proposed management on the habitats of the modelled species. Since the preferred or optimal habitats of each of the 16 indicator species are predicted to represent a different range of vegetation communities (Bonar *et al.* 1990), the response to a single management scenario will usually vary among species. If the predicted supply of habitat for a species is judged to be unacceptably high or low, then a different management scenario can be proposed and modelled. An HSI modelling approach may be useful for species whose future populations are of interest, such as socially or economically important species and rare species. HSI models, accompanied by population models for individual species, would facilitate "fine filter" management of that species (Hunter 1990).

However, for the 16 indicator species (Bonar *et al.* 1990), the habitat conditions described by each model, rather than the species themselves, are the parameters of interest. In other words, indicator species for which HSI models are developed (*e.g.*, Varied Thrush) are not of greater interest than non-modelled species (*e.g.*, Yellow-bellied Flycatcher). The modelling process also assumes that the combined range of habitats predicted to be suitable for the combination of all modelled vertebrate species will incorporate the range required by all non-modelled vertebrate species (Bonar *et al.* 1990). This assumption is not supported by available data (*e.g.*, Block *et al.* 1986), and there is little evidence that an HSI model for a species will accurately predict population changes of other species (Landres 1983, Verner 1984, Landres *et al.* 1988). In addition, extrapolating the response to habitat variation of one species to other species is "difficult or impossible" (Landres *et al.* 1988:319) because each species has unique requirements for feeding, reproduction and other life processes. Baker and Schonewald-Cox (1986:74, in Landres *et al.* 1988) cautioned that "incorrectly assuming that other species are receiving protection as a result of the protection of [an indicator] can result in the inadvertent loss of those other species".

The application of HSI models in a habitat supply analysis context is to calculate the total supply of habitat, which includes both optimal (*i.e.*, "representative") habitat and sub-optimal habitat (Bonar *et al.* 1990). Thus, unless optimal or representative habitat is somehow distinguished from sub-optimal habitat, the relative proportions of the forest types represented by each species are unknown. This makes it difficult to apply HSI models for indicator species to the problem of conserving future habitat diversity. Many combinations of stand attributes, and an even greater range of ecosystem conditions, can result in an identical HSI value, obscuring the conditions associated with a given combination of modelled habitats. It is impossible to use habitat supply analyses to report basic changes in forest conditions such as the age class distribution of different natural regions or ecosites. HSI models and habitat supply analyses are therefore an inadequate form of coarse filter management (Hunter 1990) because the filter is unevenly distributed across a poorly defined range of ecological conditions. Entire categories of ecosystems can fall through the pores of a filter defined on the basis of vertebrate habitats, and a selection of habitats represented by single species could exclude regionally important habitats because no species could be linked to them (Szaro and Balda 1982).

A final limitation of an HSI approach is that the habitats represented by the 16 indicator species are defined primarily by tree age, tree species composition, and other "stand" attributes (Bonar *et al.* 1990) that cannot easily be related to an ecosystem classification. Linking existing ecosystem classification schemes (*e.g.*, Corns and Annas 1986) with forest inventory classifications (R. Bonar, pers. comm.) would facilitate a landscape classification that could be modelled and monitored directly, rather than inferred through indicator species. Hunter (1990) suggested that habitats be selected and maintained on the basis of ecosystem and successional attributes (coarse filter approach), with additional habitat considerations for species likely to "fall through the cracks". Such species include those with a high degree of habitat specialization (*e.g.*, Northern Waterthrush, pers. obs), those ranging over more than one ecosystem (*e.g.*, large mammals, Noss 1990), or others such as crossbills (*Loxia* spp.) that are highly dependent on a single, fluctuating resource (conifer cones, Benkman 1993). Combining a coarse filter approach with a fine filter approach may provide a comprehensive framework from which to make forest management decisions.

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Table 3.1. Original (Bonar *et al.* 1990) and revised (this study) HSI models for Varied Thrush, Ovenbird and Red Squirrel. Suitability Index (S1, S2, S3, S4) relationships are given in Fig. 3.9. Mean residuals are the absolute difference between observed abundance in each HSI category and that expected if relative abundance was directly proportional to habitat suitability (Figs 3.6 - 3.9).

	Varied Thrush	Ovenbird	Red Squirrel
Original Models			
S1	Tree canopy closure	Tree canopy closure	Tree canopy closure
S2	% Spruce and fir	% Deciduous trees	% Coniferous trees
S3	Tree age	Tree age	Tree age
S4	-	-	% Spruce
Function	$(S1 \times S2)^{(1/2)} \times S3$	$S1 \times S2 \times S3$	$S1 \times (0.5 \times S2 + 0.5 \times S3) + 0.2 \times S4$
Mean Residuals			
Unlogged	0.34	0.89	0.20
Logged	0.03	0.05	0.06
Revised Models			
S1	Tree canopy closure	Tree canopy closure	Tree canopy closure
S2	% Spruce and fir	% Deciduous trees	% Coniferous trees
S3	Tree age	Tree age	Tree age
S4	-	-	% Spruce
Function	$S1 \times S2 \times S3$	$S1 \times S2 \times S3$	$S1 \times (0.4 \times S2 + 0.4 \times S3) + 0.2 \times S4$
Mean Residuals			
Unlogged	0.09	0.08	0.14
Logged	0.02	0.10	0.09

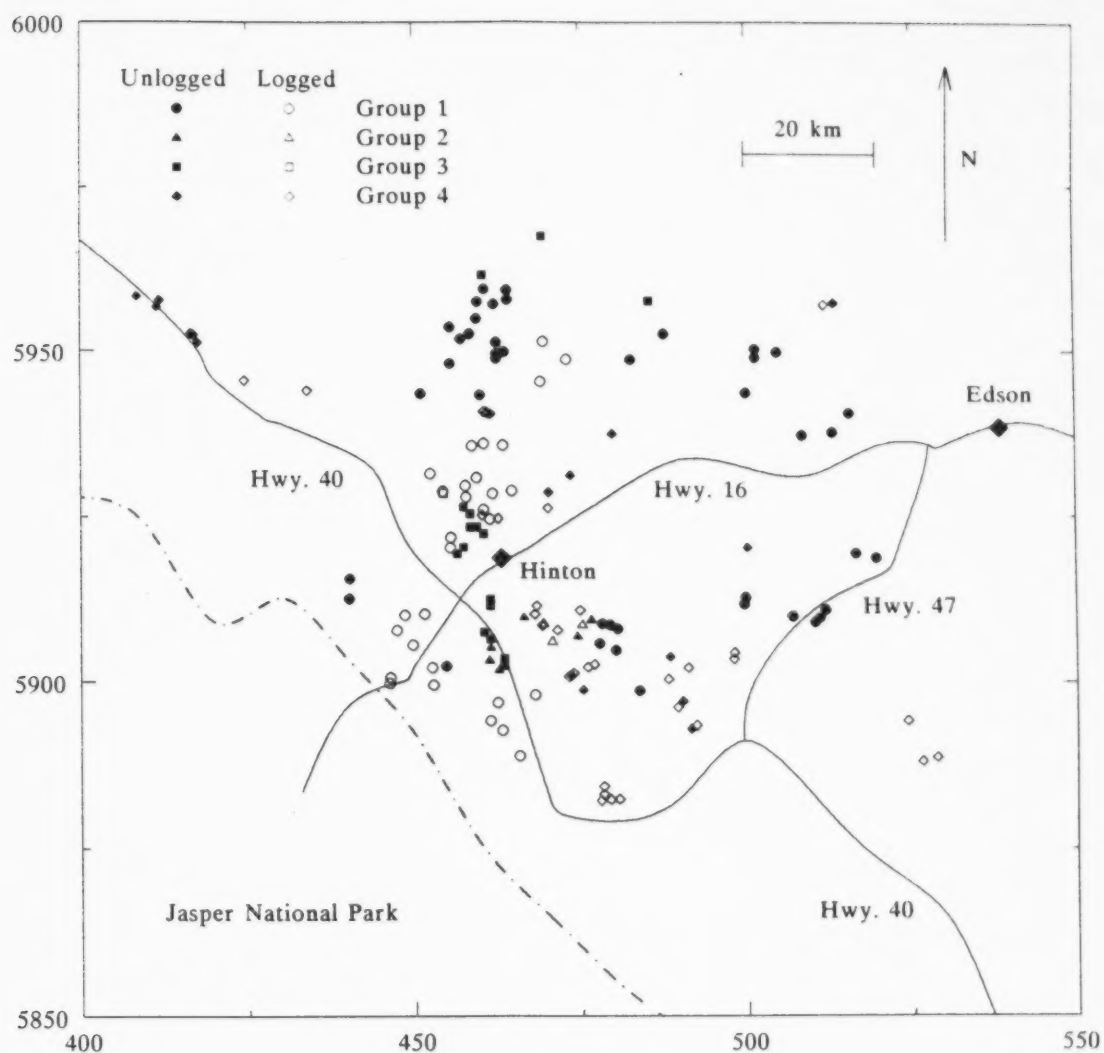


Figure 3.1. Map of the study area, indicating locations of 147 sampling sites. Each site consists of one or more sample plots, and group numbers are described in the text. Axis labels are UTM references.

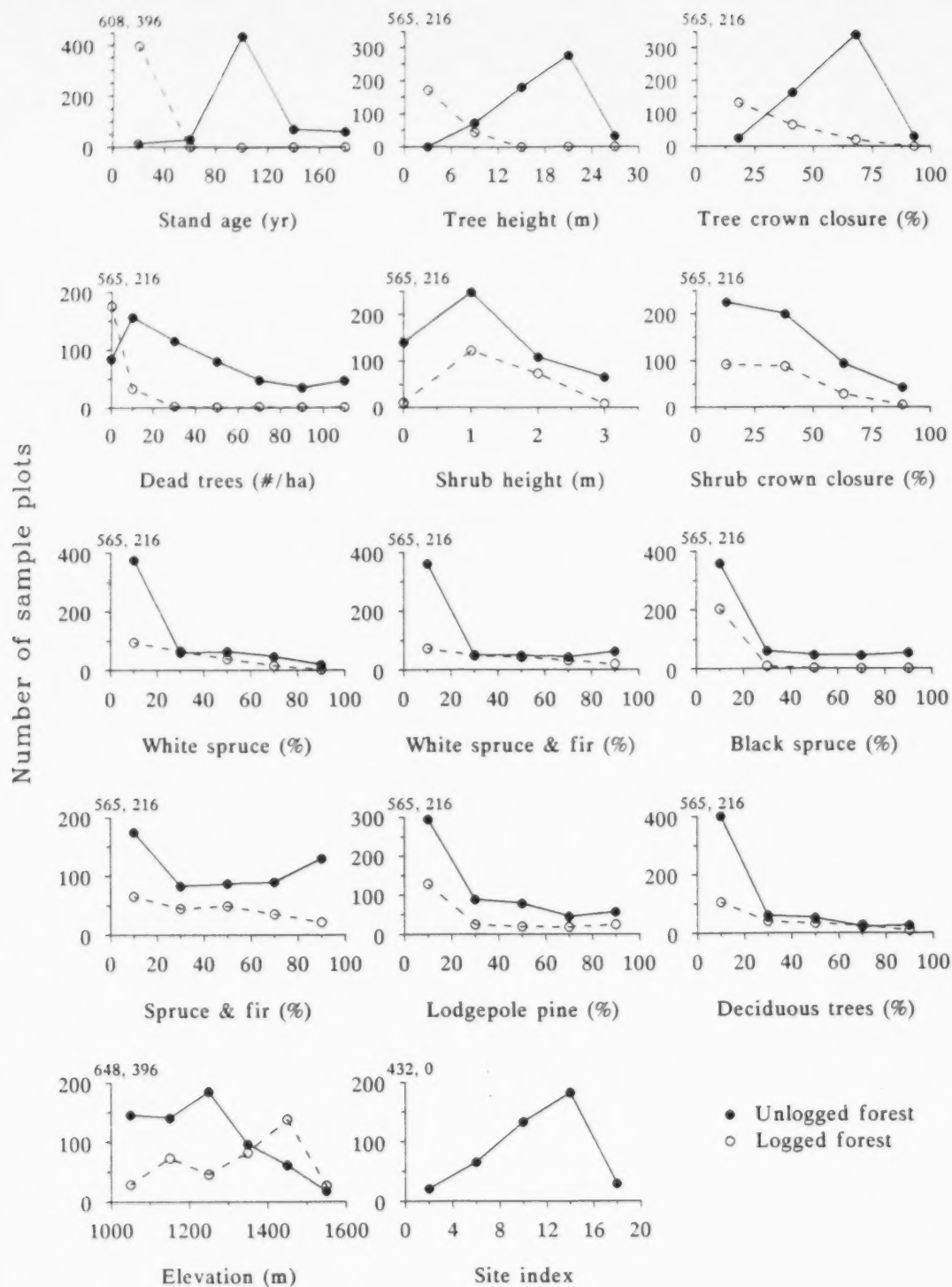


Figure 3.2. Distribution of sample sizes among classes of 14 habitat variables estimated in sample plots. The two numbers at the top of each vertical axis (separated by comma) indicate the total number of sample plots in unlogged forest and logged forest, respectively.

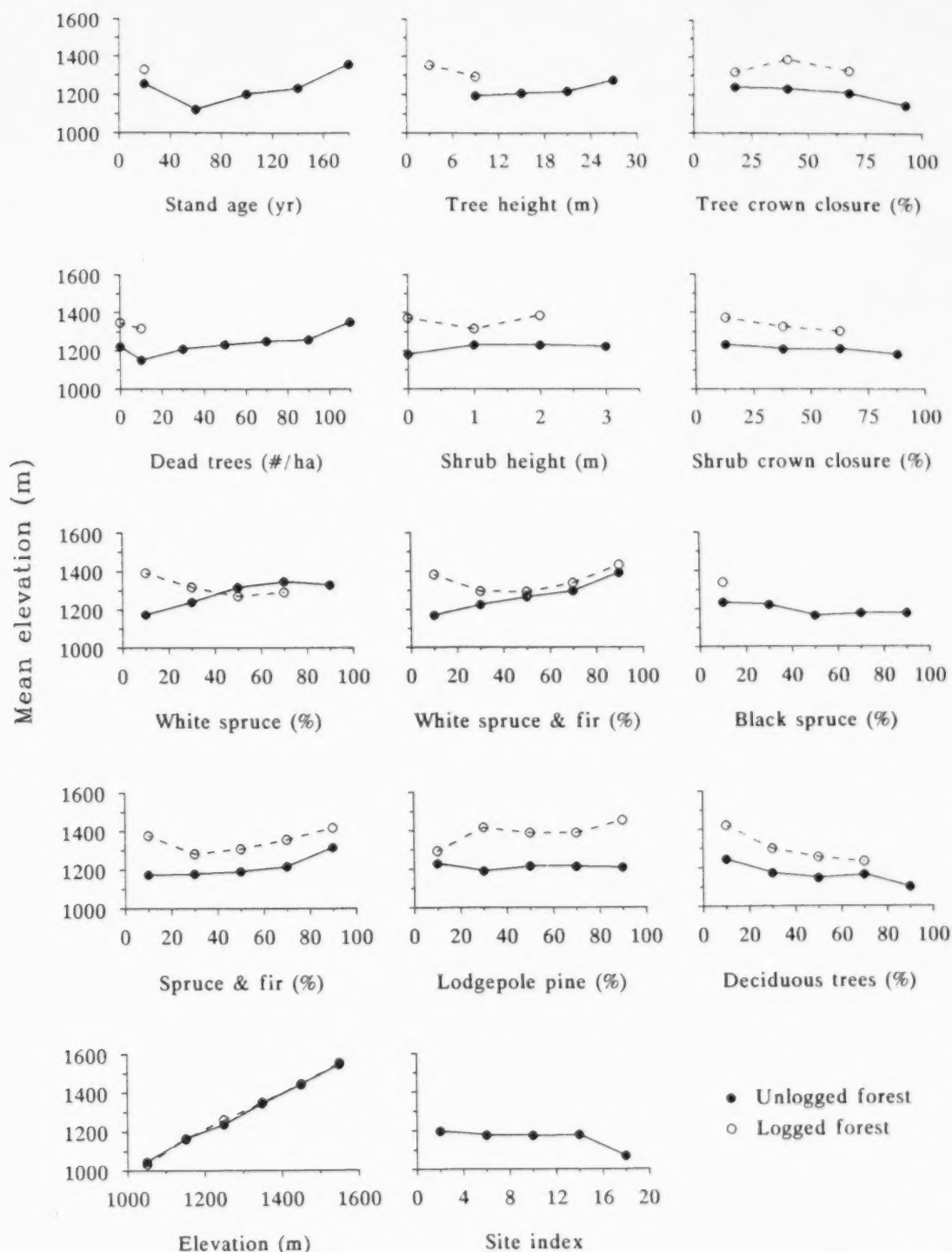


Figure 3.3. Mean elevation in each class of 14 habitat variables estimated in sample plots. Sample sizes as in Fig. 3.2.

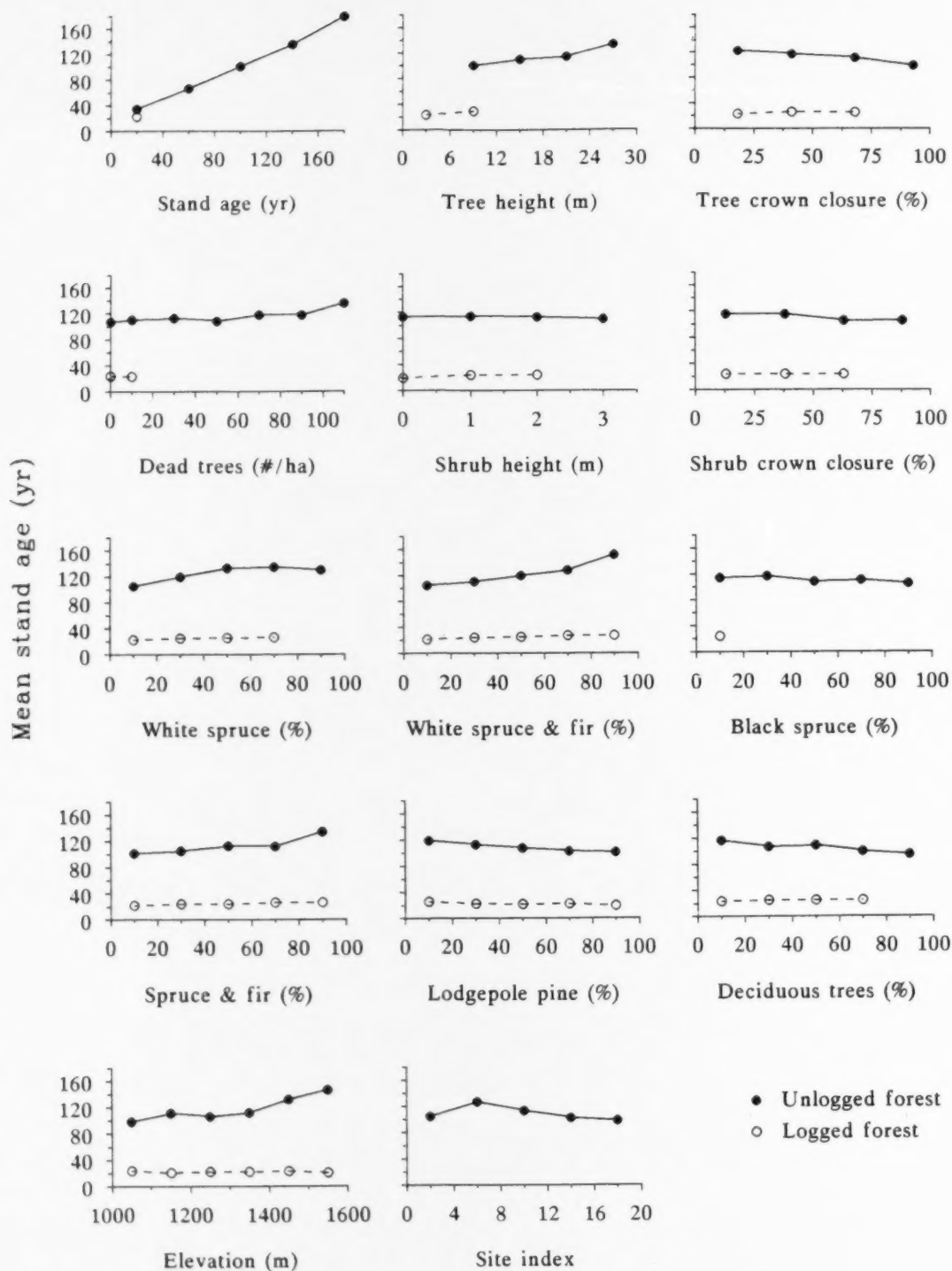


Figure 3.4. Mean stand age in each class of 14 habitat variables estimated in sample plots. Sample sizes as in Fig. 3.2.

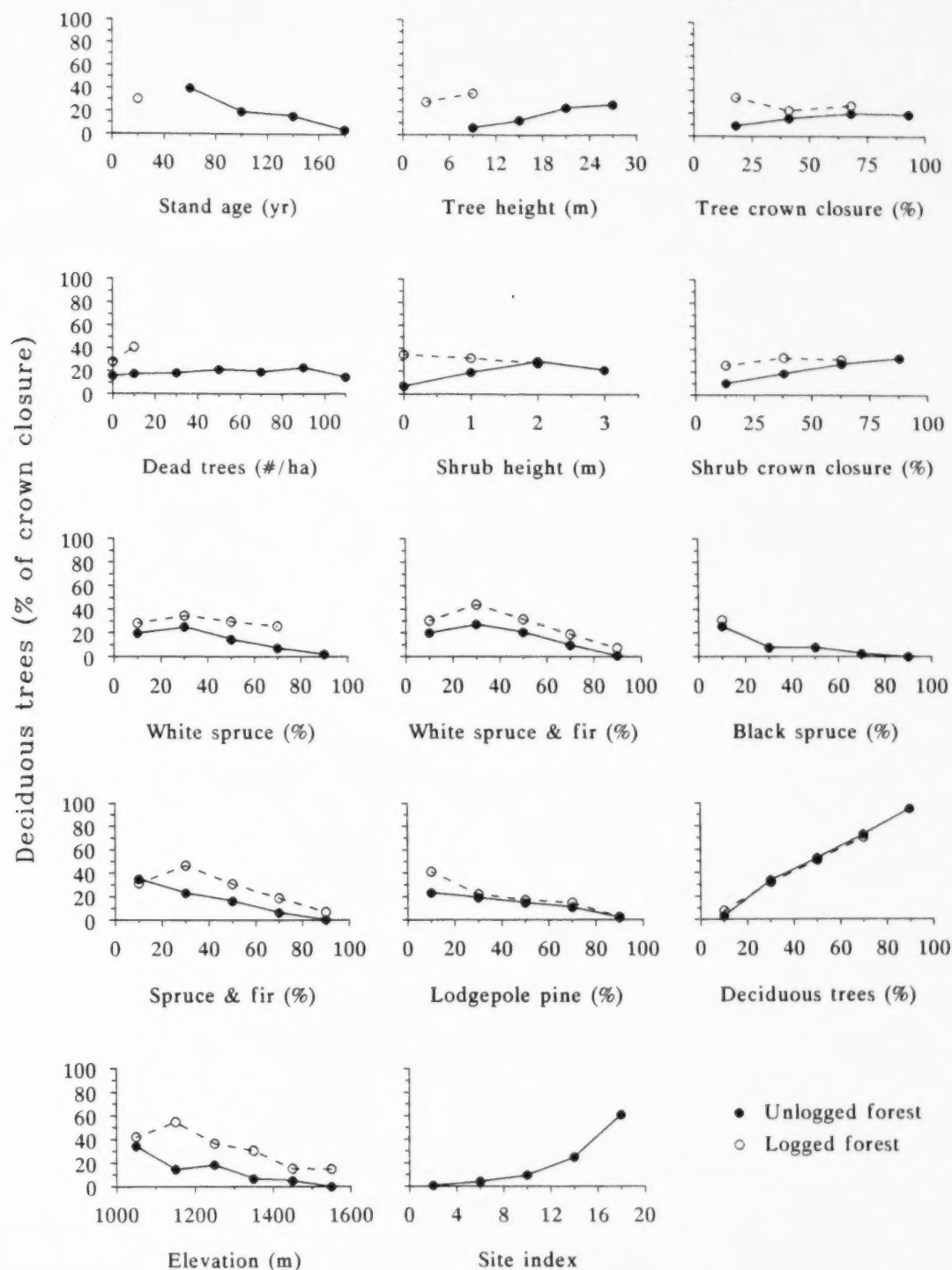


Figure 3.5. Mean proportion of deciduous trees in each class of 14 habitat variables estimated in sample plots. Sample sizes as in Fig. 3.2.

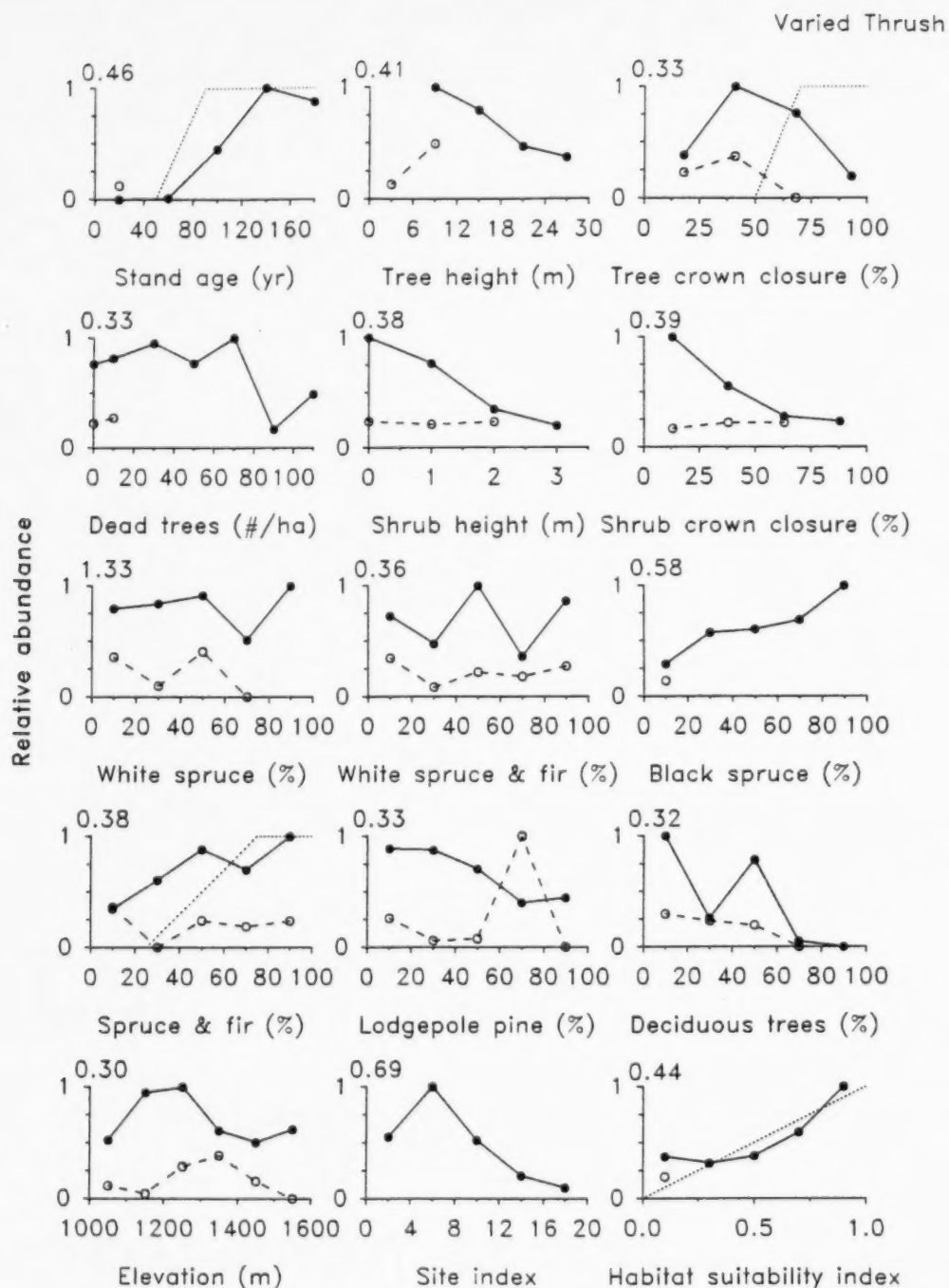


Figure 3.6. Relationships between abundance and habitat variables for Varied Thrush. Abundance (mean number of observations per 10 min. sample period) is expressed as proportion of maximum; maximum abundance is given above vertical axis. Sample sizes as in Fig. 3.2. Dotted lines represent relationships given in original HSI model (Bonar *et al.* 1990).
 • = unlogged forest ○ = logged forest

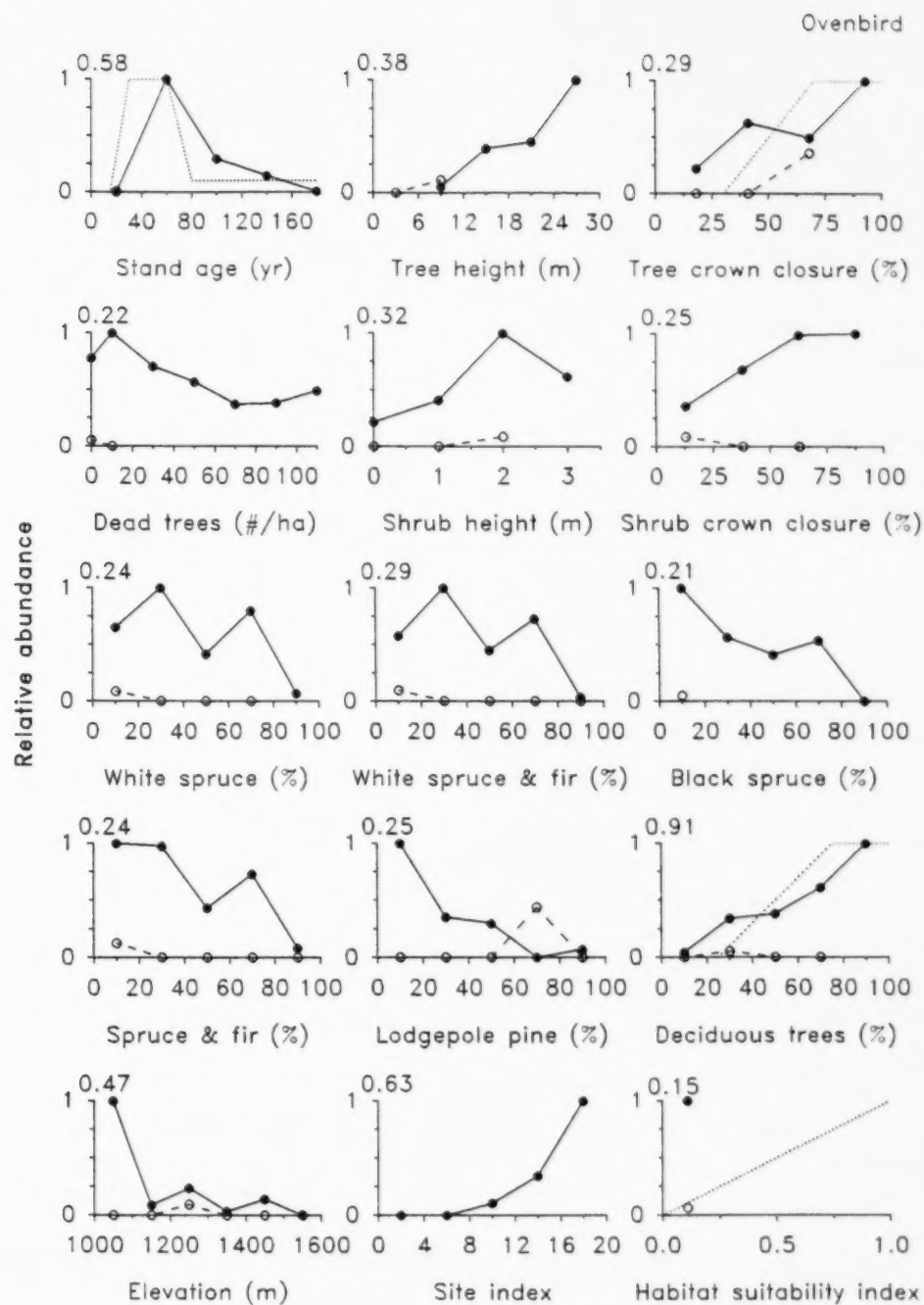


Figure 3.7. Relationships between abundance and habitat variables for Ovenbird. Abundance (mean number of observations per 10 min. sample period) is expressed as proportion of maximum; maximum abundance is given above vertical axis. Sample sizes as in Fig. 3.2. Dotted lines represent relationships given in original HSI model (Bonar *et al.* 1990).

• = unlogged forest ○ = logged forest

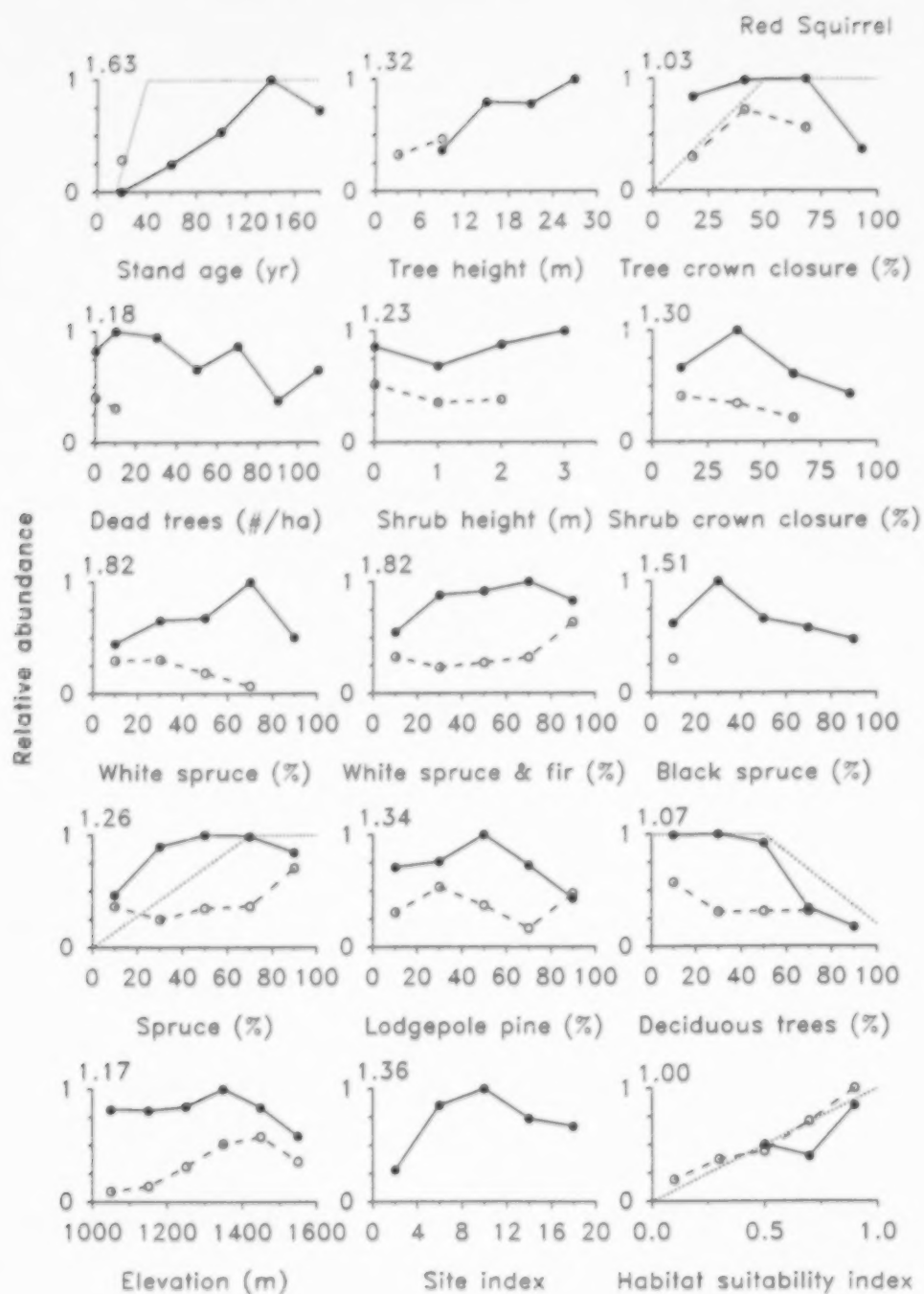


Figure 3.8. Relationships between abundance and habitat variables for Red Squirrel. Abundance (mean number of observations per 10 min. sample period) is expressed as proportion of maximum; maximum abundance is given above vertical axis. Sample sizes as in Fig. 3.2. Dotted lines represent relationships given in original HSI model (Bonar *et al.* 1990).
 • = unlogged forest ○ = logged forest

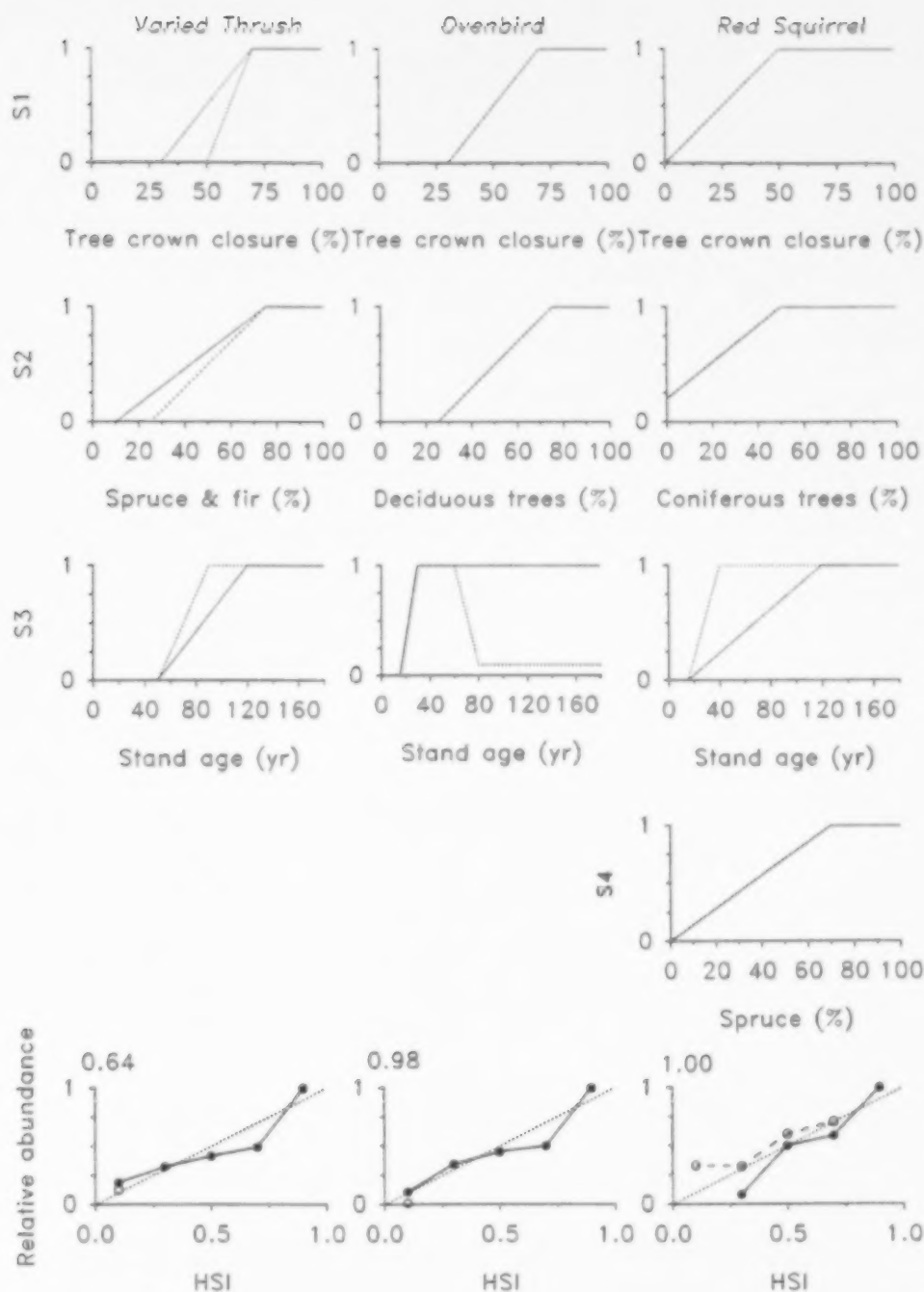


Figure 3.9. Revised suitability index relationships for Varied Thrush, Ovenbird and Red Squirrel. In upper 4 rows, dashed lines represent relationships in original HSI models (Bonar *et al.* 1990), solid lines represent revisions (this study). In bottom row, abundance (mean number of observations per 10 min. sample period) is expressed as proportion of maximum; maximum abundance is given above vertical axis.

• = unlogged forest ○ = logged forest.

4 General discussion and conclusions

The findings and discussion presented in this thesis support the hypothesis that older spruce forest communities provide habitat for at least 2 bird species (Winter Wren, Brown Creeper) that may not be available in younger stands. However, the use of habitat suitability index models for representative indicator species is probably not an effective strategy for sustaining habitat diversity in managed forest ecosystems. In order to maintain adequate representation of major plant communities, including older forests, managers need to implement forest conservation strategies that recognize and track the future supply of each community. Modern timber supply models (e.g., Walker 1990) assume that current forest ecosystem components (e.g., communities, species) and processes (e.g., nutrient cycling, soil formation) that produce wood fibre will continue to persist and function under forest management, thereby permitting a sustained supply of wood products. However, if wood production targets and harvest rates are based on an economic rotation period rather than an ecological disturbance frequency, then a sustained "supply" of other ecosystem elements such as old forest communities may be impaired. In pre-industrial forests, the probability of disturbance such as fire is influenced by elevation (Tande 1979), moisture regime, location, and chance (Rowe and Scotter 1973). In post-industrial forests, the probability of disturbance by harvesting is determined by harvest sequencing protocols that sustain a desired fibre production level (e.g., annual allowable cut). Disturbance frequency becomes less variable, and produces a truncated and more even age class structure than that resulting from ecological processes alone (Crossley 1978).

Changes in disturbance regimes that truncate forest age class distributions directly impact ecosystem composition at the community scale (Noss 1990), with indirect effects at other scales such as species that require older forests to maintain regional populations (Thompson and Welsh 1993). In other words, reducing the area of old forest reduces community-scale biodiversity, and may affect other aspects of ecosystem composition, structure, and function. Reducing biodiversity at this scale is inconsistent with Canada's National Forest Strategy, which aims to maintain the integrity of forest ecosystems, including old forest (Canadian Council of Forest Ministers 1992), although integrity, old-growth, and the implied ecosystem scale are not clearly defined in the strategy. Dancik *et al.* (1990) identified old-growth communities as elements that should be maintained within Alberta's managed forest ecosystems.

Strategies and policies for maintaining older age classes within managed forest ecosystems are being developed in many regions. The following discussion outlines the design considerations for an old-growth management policy for west-central Alberta. This discussion rests on 3 assumptions: 1) maintaining a perpetual supply of old forest communities is a goal of forest ecosystem management (*sensu* Grumbine 1994); 2) meeting that goal is possible by attempting to integrate known ecological processes into existing management plans; and 3) the logical framework for an old forest management policy is derived from consideration of dynamic ecological processes rather than by reference to a specified pre-industrial "state" or pattern.

The major design considerations for an old-growth management policy in this region are as follows.

1) *Disturbance frequency and age class distribution:* Prior to effective fire suppression, forest age classes in this region followed a negative exponential distribution, a pattern generated by frequent fires accompanied by variable disturbance probabilities across the landscape (Heinselman 1981, Van Wagner 1978, Telfer 1993). Incorporating variable disturbance frequencies into harvest

planning would more closely emulate natural disturbance patterns than existing harvest sequencing protocols (Crossley 1978, Walker 1990).

2) *Disturbance size and the size of old forest communities*: The distribution of fire sizes in unmanaged boreal forest ecosystems also follows a negative exponential distribution, with many small fires and a few large fires, but with most of the forest area in a given location originating from large fires (Hunter 1993, Telfer 1993). At a regional scale, the management system in west-central Alberta may roughly approximate historical disturbance sizes. In the 1950's the area was divided into operational compartments, within which stand ages were relatively uniform (Crossley 1978). There are currently 136 compartments, ranging in area from 200 to 17,000 ha, averaging 7,600 ha (Weldwood of Canada 1992). Compartments are scheduled for harvesting on a priority basis determined by consideration of stand age and proximity to the mill (Weldwood of Canada 1992), and usually two-pass clearcutting of merchantable stands is completed within a 20 year "open" period. Within compartments, the variable proportions of unproductive forest or buffer areas that remain after harvesting may produce patterns similar to those resulting from fire "skipping" behaviour and incomplete burning in most boreal forest systems (Kelsall *et al.* 1977).

If the scale and intensity of disturbance within compartments is considered to be analogous to historical disturbances by fire, then the new disturbance regime follows a size distribution equal to that of the compartment sizes. Although the distribution of compartment sizes does not follow a negative exponential distribution (Weldwood of Canada 1992), a few large disturbances could be simulated by synchronizing harvesting in adjacent compartments. Compartments or compartment groups could provide old forest communities through extended harvest rotations, and may also be sufficiently large to permit considerable beta- or among-habitat diversity arising from topographic relief and edaphic variation within a single age class.

3) *Location and arrangement of old forest communities*: Differences in probability of disturbance among locations in pre-industrial forest ecosystems influenced the spatial distribution of age classes, including old forest (Sousa 1984). For example, Tande (1979) found that the proportion of older forest increased with elevation in the Jasper area. The distribution of old forest patches in managed systems could also be guided by topographic considerations, locating them in regions with inherently lower fire probabilities. However, older forests are present throughout west-central Alberta, not exclusively at higher elevations, and other criteria may need to be used to locate older patches. Regional diversity would be increased by locating older forest communities throughout the area, perhaps in each of the major forest sections (Rowe 1972) or ecoregions (Corns and Annas 1986), thereby fostering the range of old forest communities that develop in different climatic and topographic situations (Corns and Annas 1986). It may also be useful to prioritize ecoregions based on their representation within the FMA area relative to adjacent jurisdictions. For example, locating old forest communities in the Subalpine Forest Section may be of low priority because extensive Subalpine forests occur in nearby Jasper National Park (Rowe 1972). An analysis of the relative representation of different ecoregions within the FMA area would assist in setting such priorities.

4) *Total area of old forest communities*: Reliance on ecological knowledge to set criteria for total area of old forest is difficult because of insufficient data on disturbance probabilities in pre-industrial forest ecosystems. In 1911, approximately 15 % of the productive forest was older than 80 years, with 3% older than 160 years (Van Wagner 1978). Whether this "snapshot" is typical of the region's history is unknown. Proportions increased to 21% older than 80 years and 6% older than 160 years by 1956, possibly in part due to increased fire suppression activities (Van Wagner 1978). Historically, ecological disturbance probabilities have likely been increasing since the end of the

Little Ice Age (1350-1870 AD), during which summers were shorter and cooler than they are now (Pielou 1991). Climatic changes at this temporal scale may have large effects on forest age class distributions, although they may always have approximated a negative exponential curve. It may not be possible to determine the "optimal" or "natural" area of older age classes in future managed forests. However, the continued harvesting of older forests, and the planning of future fibre supply based on economic rotation periods alone, would simplify ecosystem composition and structure considerably.

5) *Summary*: Integrating known ecological processes with current management strategies to provide for old forest communities in west-central Alberta could be accomplished by designating selected operational compartments as extended rotation compartments. Regional diversity of old forest communities would be greater if the compartments were located throughout the FMA area, with locations prioritized on the basis of regional representation in each ecological region. Since compartments average 0.7% of the FMA area, several extended rotation compartments would be required to emulate the 1911 or 1956 area of old forest, or to meet provincial guidelines of "10% mature / overmature forest" (Alberta Environmental Protection 1994:26). While reference to a pre-industrial "state" may be inappropriate, dramatic deviation from known disturbance regimes would reduce regional biodiversity, compromise ecosystem integrity, and reduce options for alternative forest uses.

The development of forestry practices that attempt to maintain ecosystem integrity is consistent with Aldo Leopold's (1966) extension of ethical responsibility to the larger biotic community of which human beings form a part. The evolution of a land ethic based on the premise that individuals are members of a "community of interdependent parts" (Leopold 1966:239) and considered by Leopold to be an ecological necessity, would promote increased respect for natural ecosystem components, structures and processes.

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Appendix 1. List of all bird species observed in Chapter 2, with scientific names, migratory pattern, foraging mode and nest location. Species in parentheses were not observed during sampling within 150 m. Four-letter codes are given only for species referred to by codes in Chapter 2.

Migratory pattern: Permanent Resident, Short-Distance migrant, Long-Distance migrant.

Foraging mode: Aerial Insectivore, Ground Gleaner, Foliage Gleaner, Bark Gleaner, Other.

Nest location: Ground, Shrubs or Trees, Trees (Coniferous), Trees (Deciduous),

Trees (both), tree Cavity.

Code	Common Name	Scientific Name	Migratory Pattern	Foraging Mode	Nest Location
RUGR	Common Snipe	<i>Gallinago gallinago</i>	SD	GG	GR
	Solitary Sandpiper	<i>Tringa solitaria</i>	LD	GG	TR
	Northern Goshawk	<i>Accipitor gentilis</i>	PR	OT	TR
	Ruffed Grouse	<i>Bonasa umbellus</i>	PR	GG	GR
	Spruce Grouse	<i>Dendragapus canadensis</i>	PR	GG	GR
	Northern Flicker	<i>Colaptes auratus</i>	SD	GG	CA
TTWO	Three-toed Woodpecker	<i>Picoides tridactylus</i>	PR	BG	CA
	Pileated Woodpecker	<i>Dryocopus pileatus</i>	PR	BG	CA
	Olive-sided Flycatcher	<i>Contopus borealis</i>	LD	AI	TC
	Western Wood-Pewee	<i>Contopus sordidulus</i>	LD	AI	TC
	Least Flycatcher	<i>Empidonax minimus</i>	SD	AI	TD
	Alder Flycatcher	<i>Empidonax alnorum</i>	LD	AI	ST
YBFL	Yellow-bellied Flycatcher	<i>Empidonax flaviventris</i>	LD	AI	GR
GRJA	Gray Jay	<i>Perisoreus canadensis</i>	PR	FG	TC
	Common Raven	<i>Corvus corax</i>	PR	GG	TR
	Black-capped Chickadee	<i>Parus atricapillus</i>	PR	FG	CA
BOCH	Boreal Chickadee	<i>Parus hudsonicus</i>	PR	FG	CA
BRCR	Brown Creeper	<i>Certhia americana</i>	PR	BG	CA
RBNU	Red-breasted Nuthatch	<i>Sitta canadensis</i>	PR	BG	CA
WIWR	Winter Wren	<i>Troglodytes troglodytes</i>	SD	GG	GR
GCKI	Golden-crowned Kinglet	<i>Regulus satrapa</i>	SD	FG	TC
RCKI	Ruby-crowned Kinglet	<i>Regulus calendula</i>	SD	FG	TC
	Townsend's Solitaire	<i>Myadestes Townsendi</i>	SD	AI	GR
SWTH	Swainson's Thrush	<i>Catharus ustulatus</i>	LD	FG	ST
HETH	Hermit Thrush	<i>Catharus guttatus</i>	SD	GG	GR
VATH	Varied Thrush	<i>Ixorius naevius</i>	SD	GG	TC
AMRO	American Robin	<i>Turdus migratorius</i>	SD	GG	ST
	Bohemian Waxwing	<i>Bombycilla garrulus</i>	PR	FG	TC
	Cedar Waxwing	<i>Bombycilla cedrorum</i>	SD	FG	TR
	Solitary Vireo	<i>Vireo solitarius</i>	LD	FG	TC
WAVI	Warbling Vireo	<i>Vireo gilvus</i>	LD	FG	TD
TEWA	Tennessee Warbler	<i>Vermivora peregrina</i>	LD	FG	GR
OCWA	Orange-crowned Warbler	<i>Vermivora celata</i>	SD	FG	GR
	Magnolia Warbler	<i>Dendroica magnolia</i>	LD	FG	TC
YRWA	Yellow-rumped Warbler	<i>Dendroica coronata</i>	SD	FG	TC
WIWA	Wilson's Warbler	<i>Wilsonia pusilla</i>	LD	FG	GR
	Savannah Sparrow	<i>Passerculus sandwichensis</i>	SD	GG	GR

Code	Common Name	Scientific Name	Migratory Pattern	Foraging Mode	Nest Location
CHSP	Chipping Sparrow	<i>Spizella passerina</i>	SD	GG	ST
	Clay-colored Sparrow	<i>Spizella pallida</i>	LD	GG	ST
DEJU	Dark-eyed Junco	<i>Junco hyemalis</i>	SD	GG	GR
WTSP	White-throated Sparrow	<i>Zonotrichia albicollis</i>	SD	GG	GR
LISP	Lincoln's Sparrow	<i>Melospiza lincolnii</i>	LD	GG	GR
	Western Tanager	<i>Piranga ludoviciana</i>	LD	FG	TC
	Pine Siskin	<i>Carduelis pinus</i>	SD	FG	TC
WWCR	White-winged Crossbill	<i>Loxia leucoptera</i>	PR	FG	TC
PIGR	Pine Grosbeak	<i>Pinicola enucleator</i>	PR	FG	TC
	(American Crow)	<i>Corvus brachyrhynchos</i>			
	(Brown-headed Cowbird)	<i>Molothrus ater</i>			
	(Canada Goose)	<i>Branta canadensis</i>			
	(Common Loon)	<i>Gavia immer</i>			
	(Evening Grosbeak)	<i>Coccothraustes vespertinus</i>			
	(Great Blue Heron)	<i>Ardea herodias</i>			
	(Northern Waterthrush)	<i>Seiurus noveboracensis</i>			
	(Osprey)	<i>Pandion haliaetus</i>			
	(Ovenbird)	<i>Seiurus aurocapillus</i>			

Migratory pattern from Partners in Flight Newsletter (1992, vol. 2(1) p. 30) and pers. obs.

Foraging mode from Ehrlich et al. (1988).

Nest location from Ehrlich et al. (1988) and Peck and James (1987)

Appendix 2. Number of observations of each bird species in 3 age classes of forest in west-central Alberta, 1991 and 1992 (Chapter 2). Values are number of observations within 150 m of the plot centre. Superscripts are totals excluding plots containing residual unlogged forest.

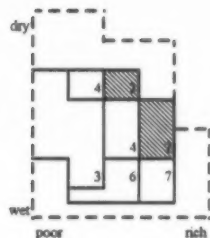
Species	Young			Mature			Old		
	1	2	3	1	2	3	1	2	3
Solitary Sandpiper	-	2 ¹	1 ¹	-	-	3	2	-	-
Common Snipe	-	-	-	-	2	-	-	-	-
Northern Goshawk	-	-	-	-	-	1	-	-	-
Ruffed Grouse	12 ¹⁰	9 ⁸	-	4	-	-	-	-	-
Spruce Grouse	-	-	-	1	1	1	-	-	1
Northern Flicker	4 ²	-	6 ⁶	-	1	-	-	-	-
Three-toed Woodpecker	3 ¹	1 ⁰	-	5	-	13	14	10	38
Pileated Woodpecker	-	-	-	1	-	-	-	-	-
unidentified woodpecker	4 ³	1 ⁰	-	2	2	-	4	-	-
Olive-sided Flycatcher	3 ⁰	-	-	-	-	-	-	-	-
Western Wood-Pewee	1 ¹	-	-	-	-	-	-	-	-
Least Flycatcher	3 ¹¹	8 ⁶	-	-	-	-	-	-	-
Alder Flycatcher	8 ³	18 ⁹	1 ¹	-	-	-	-	-	-
Yellow-bellied Flycatcher	10 ⁵	26 ¹⁸	22 ¹¹	16	14	1	-	6	-
Gray Jay	39 ²²	39 ¹⁶	42 ³⁴	27	44	32	24	37	38
Common Raven	-	-	-	-	-	-	1	3	-
Black-capped Chickadee	-	4 ³	-	4	-	-	-	2	3
Boreal Chickadee	16 ⁷	5 ²	16 ¹⁵	7	20	12	15	20	11
Brown Creeper	-	-	-	11	-	-	20	-	22
Red-breasted Nuthatch	8 ²	3 ¹	1 ¹	5	2	10	26	25	27
Winter Wren	-	-	-	7	4	-	24	15	42
Golden-crowned Kinglet	4 ¹	-	1 ⁰	38	45	33	41	53	48
Ruby-crowned Kinglet	30 ³	32 ²	19 ¹¹	24	36	31	21	50	7
Townsend's Solitaire	-	-	-	-	-	3	-	-	-
Swainson's Thrush	48 ³⁵	27 ¹⁶	108 ⁷⁴	63	76	11	17	51	10
Hermit Thrush	28 ¹⁸	12 ⁸	-	1	-	3	-	-	-
Varied Thrush	8 ⁴	9 ³	2 ¹	11	23	17	21	16	9
American Robin	28 ¹³	30 ¹²	1 ¹	-	8	8	-	-	-
Bohemian Waxwing	-	-	-	-	-	-	2	-	-
Cedar Waxwing	5 ⁴	-	-	-	-	-	-	-	-
Solitary Vireo	1 ¹	2 ¹	-	-	-	2	-	1	-
Warbling Vireo	71 ⁵⁵	52 ⁴⁰	15 ¹¹	2	3	1	-	5	-
Tennessee Warbler	3 ¹	22 ¹⁰	-	2	4	-	-	2	-
Orange-crowned Warbler	74 ⁴⁹	56 ³¹	38 ²⁵	-	4	1	-	3	-
Magnolia Warbler	1 ⁰	-	-	-	-	-	-	-	-
Yellow-rumped Warbler	136 ⁷²	113 ⁵¹	147 ⁹⁰	123	156	102	93	127	98
Wilson's Warbler	8 ¹	46 ¹⁷	33 ¹⁶	2	31	1	19	14	2
Savannah Sparrow	2 ²	-	-	-	-	-	-	-	-
Chipping Sparrow	59 ³²	45 ²²	58 ³⁹	21	64	16	32	29	19
Clay-colored Sparrow	-	-	1 ¹	-	-	-	-	-	-
Dark-eyed Junco	84 ⁴⁵	79 ³⁴	109 ⁷⁹	38	72	50	52	95	65
White-throated Sparrow	21 ¹³	23 ¹²	7 ³	1	-	-	2	-	-
Lincoln's Sparrow	6 ⁵	14 ⁴	6 ⁵	-	5	1	5	1	-
Western Tanager	-	-	-	-	-	-	-	1	-
Pine Siskin	1 ⁰	-	-	-	2	-	-	1	1
White-winged Crossbill	3 ⁰	-	-	3	23	26	15	33	22
Pine Grosbeak	1 ¹	2 ⁰	7 ⁵	1	4	3	10	10	4

Appendix 3. Bird abundance in 5 ecosystem associations of the Upper Boreal Cordilleran (UBC) ecoregion (Corns and Annas 1986), based on data from 6 mature and old sites (Chapter 2), 12 plots per site (n = 72 plots).

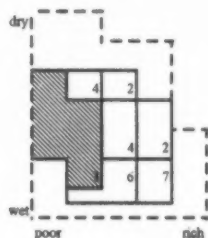
Key to ecosystem associations:

Associations were classified using the key and descriptions of Corns and Annas (1986), and are displayed on a schematic representation of moisture and nutrient availability (Figure 12 of Corns and Annas 1986). Dashed line indicates limits of ecoregion (not all ecosystem associations were sampled). Note: UBC 2 includes 15 plots classified as Subalpine 1 (Engelmann spruce - subalpine fir / feathermoss), which is similar to UBC 2 in moisture and nutrient regime but higher in elevation. n = number of plots.

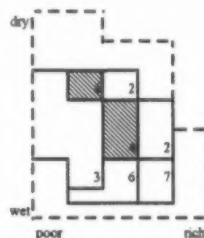
UBC 2
white spruce /
feather moss
(n = 44)



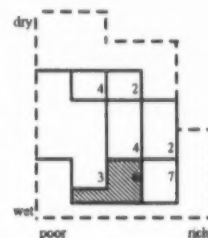
UBC 3
lodgepole pine -
black spruce /
Labrador tea /
feather moss
(n = 5)



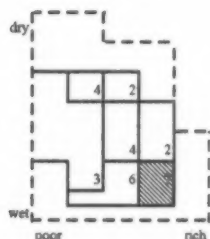
UBC 4
lodgepole pine /
alder
(n = 5)



UBC 6
black spruce /
Labrador tea /
horsetail
(n = 12)



UBC 7
white spruce /
common horsetail /
feather moss
(n = 6)



Key to bird abundance (next page):

Abundance of selected bird species, as percent of maximum

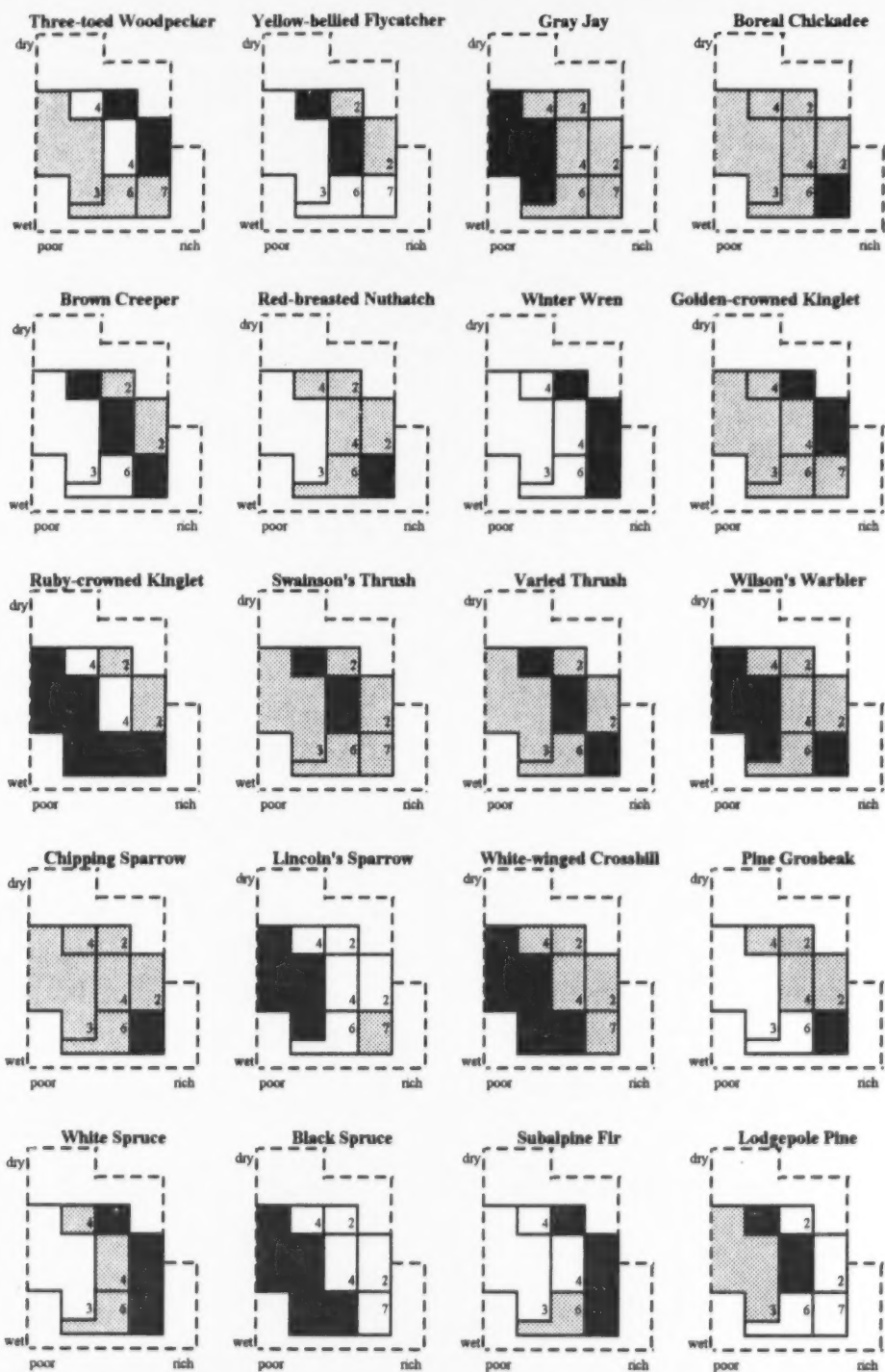
dark > 75 %
light 25 - 75 %
unshaded < 25 %

Key to tree species composition (next page):

Relative crown closure of major tree species, as percent of maximum

dark > 75 %
light 25 - 75 %
unshaded < 25 %

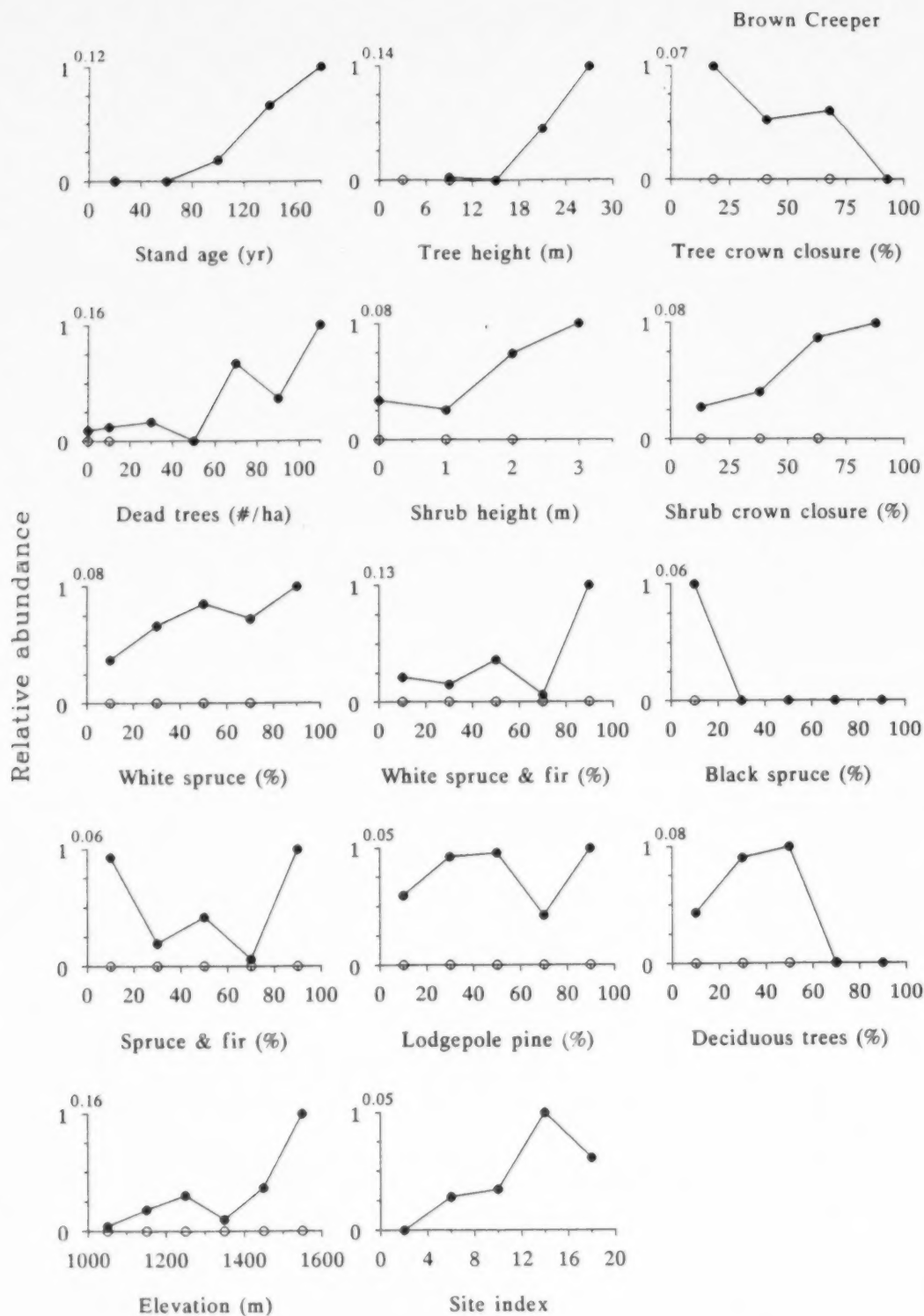
Appendix 3, continued.



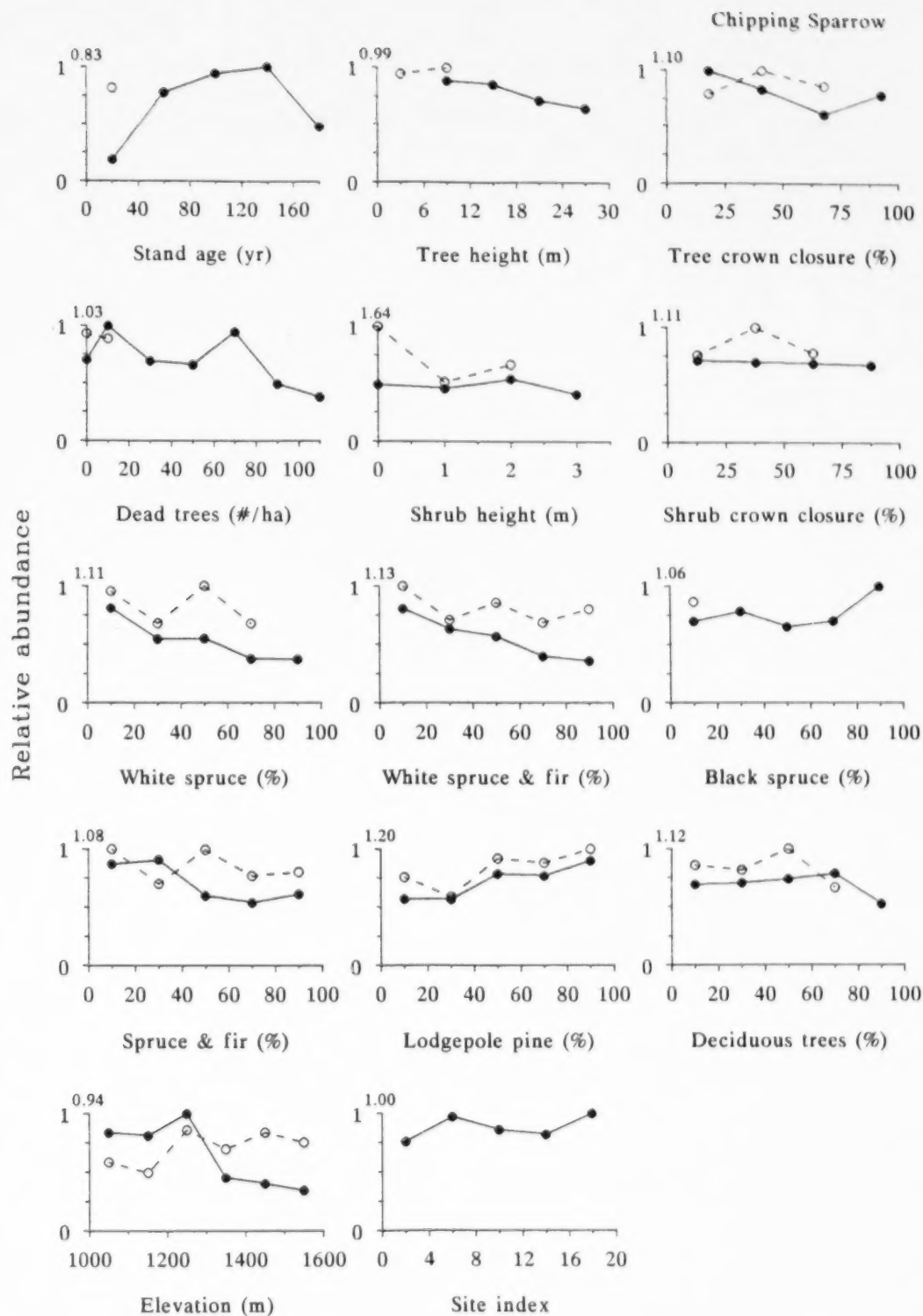
Appendix 4. Relationships between abundance and habitat variables for 12 bird species for which HSI models are to be developed (Bonar *et al.* 1990, R. Bonar, pers. comm.), from Chapter 3. Abundance (mean number of observations per 10 min. sample period) is expressed as proportion of maximum; maximum abundance is given above vertical axis. Sample sizes as in Fig. 3.2.

• = unlogged forest

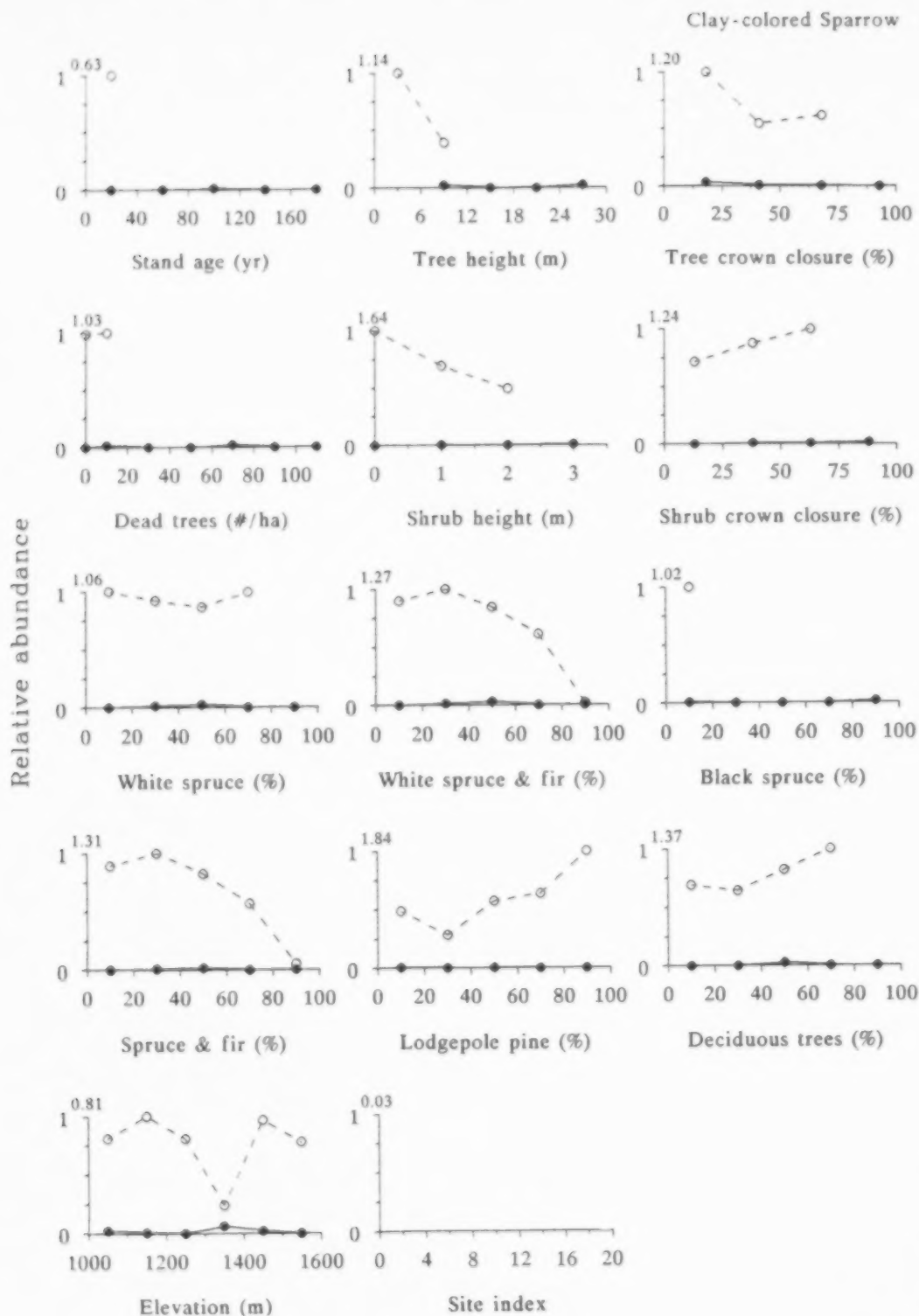
◦ = logged forest.



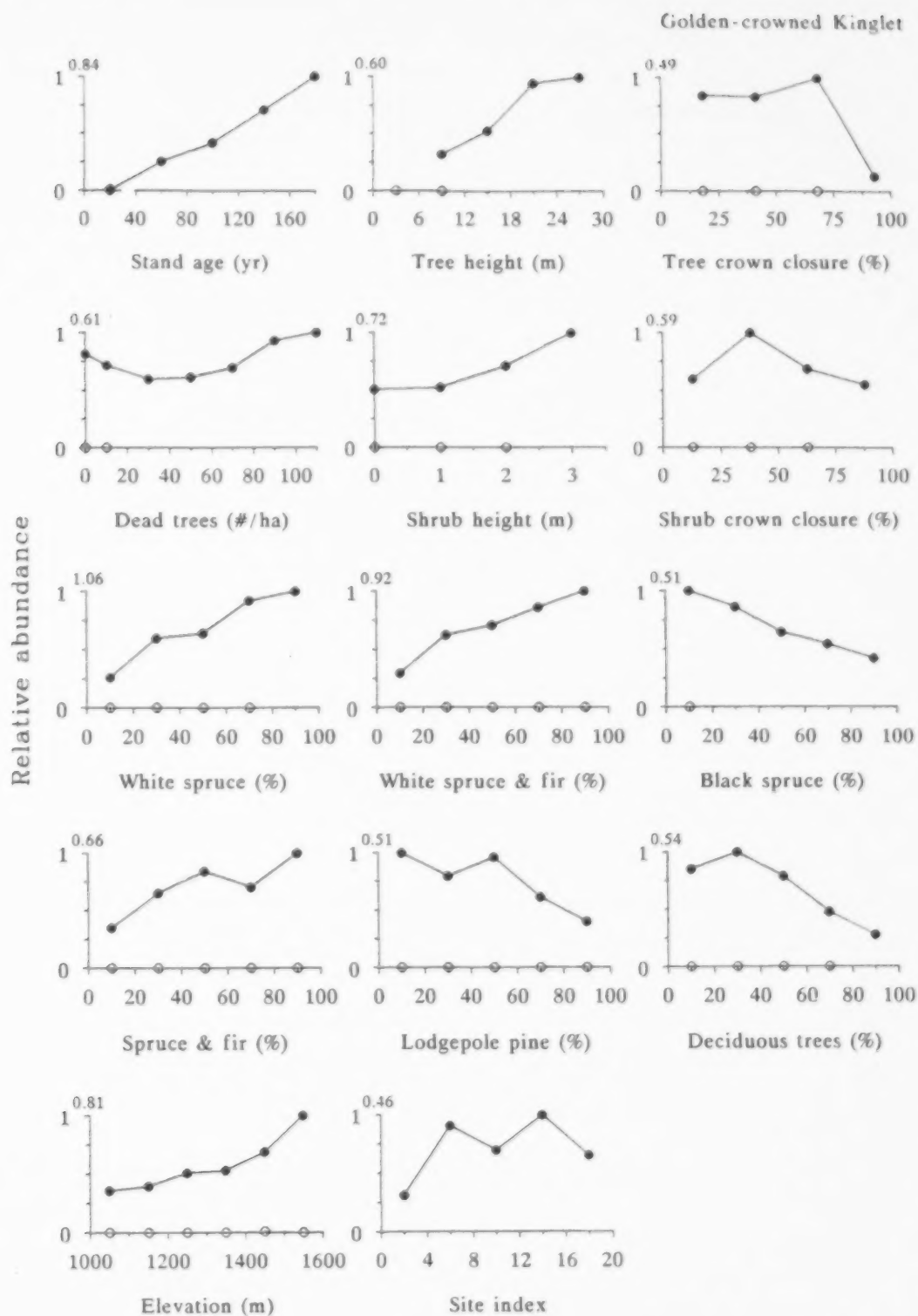
Appendix 4, continued. Relationships between abundance and habitat values for Brown Creeper.



Appendix 4, continued. Relationships between abundance and habitat values for Chipping Sparrow.

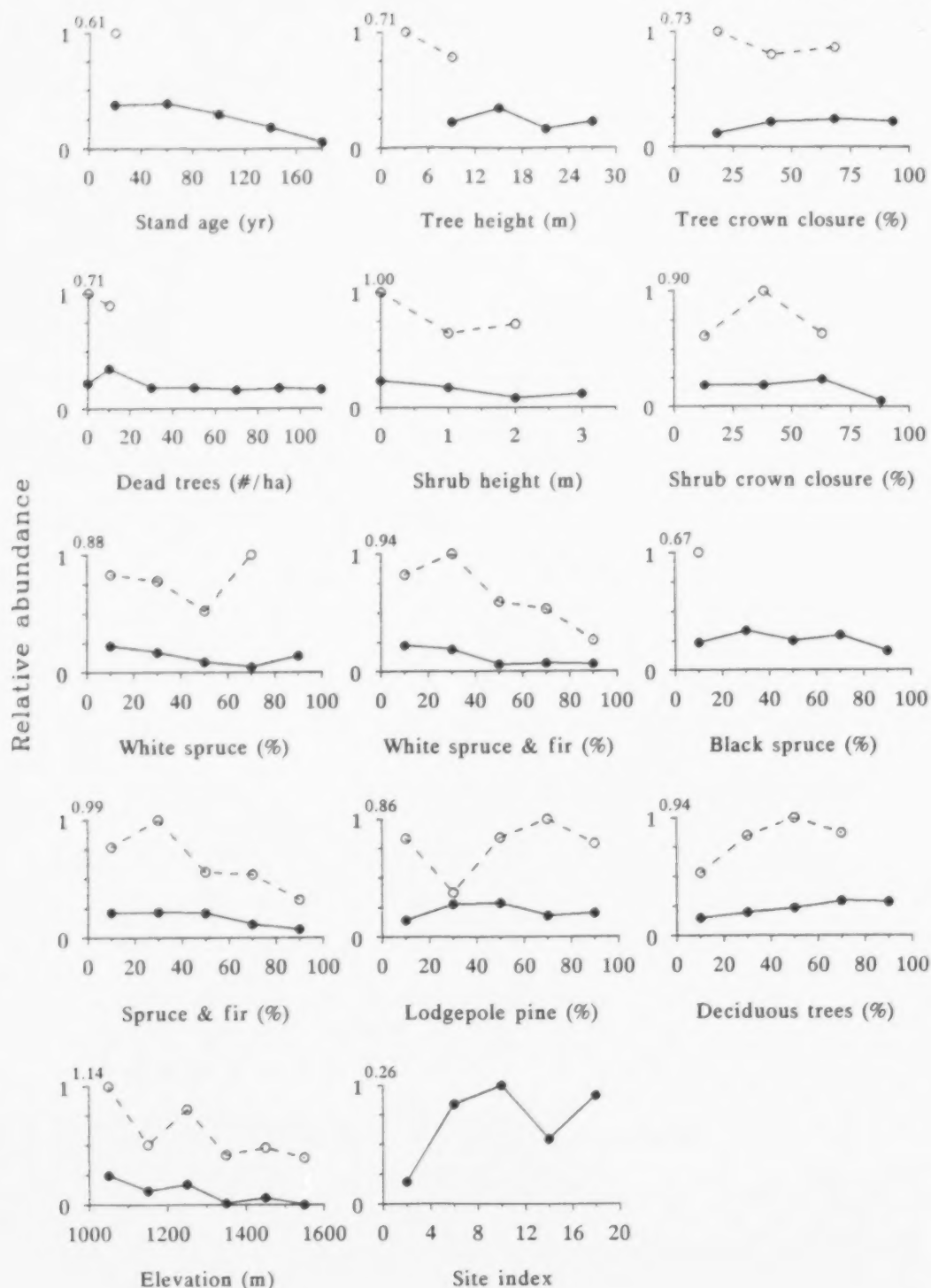


Appendix 4, continued. Relationships between abundance and habitat for Clay-colored Sparrow.

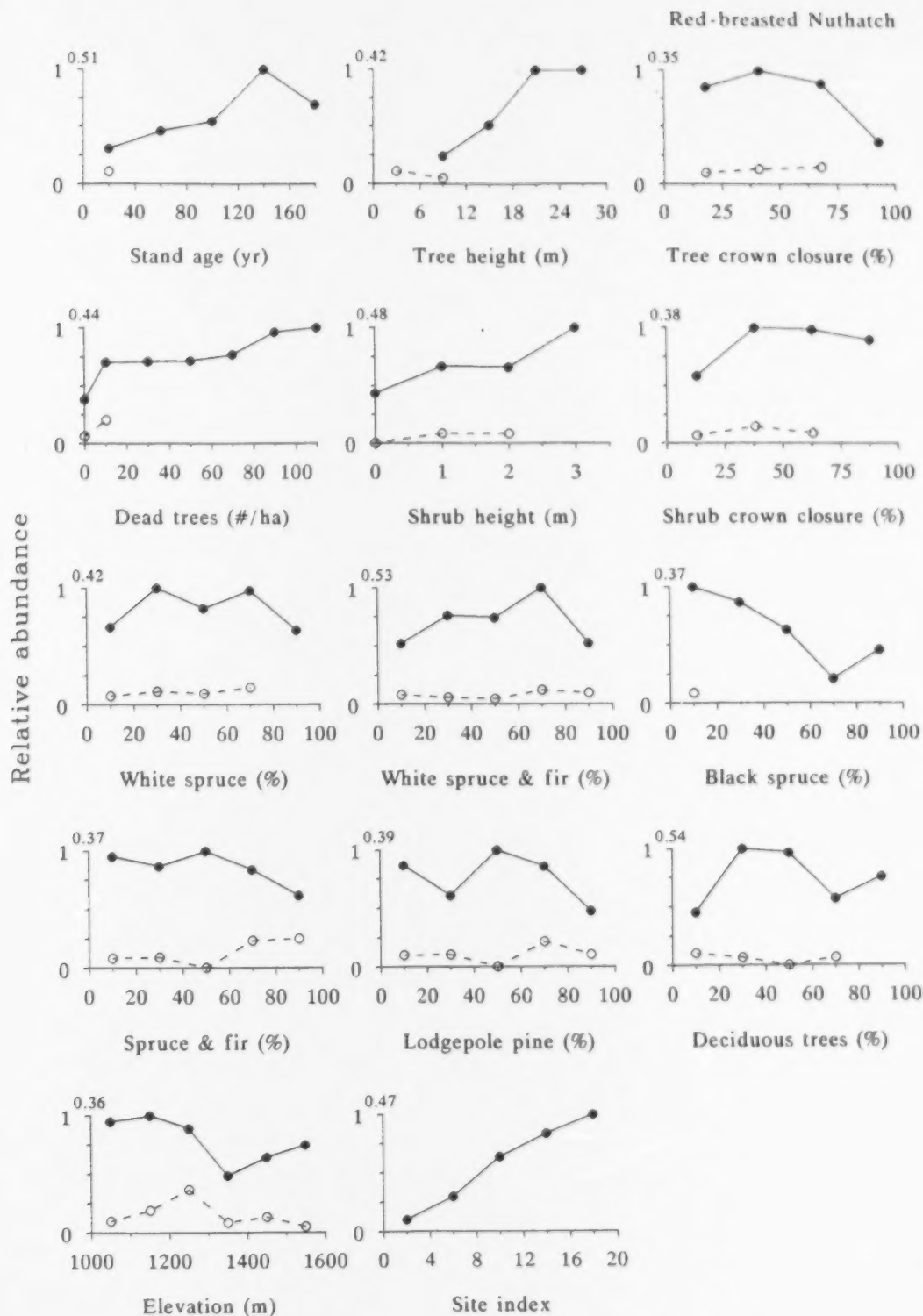


Appendix 4, continued. Relationships between abundance and habitat for Golden-crowned Kinglet.

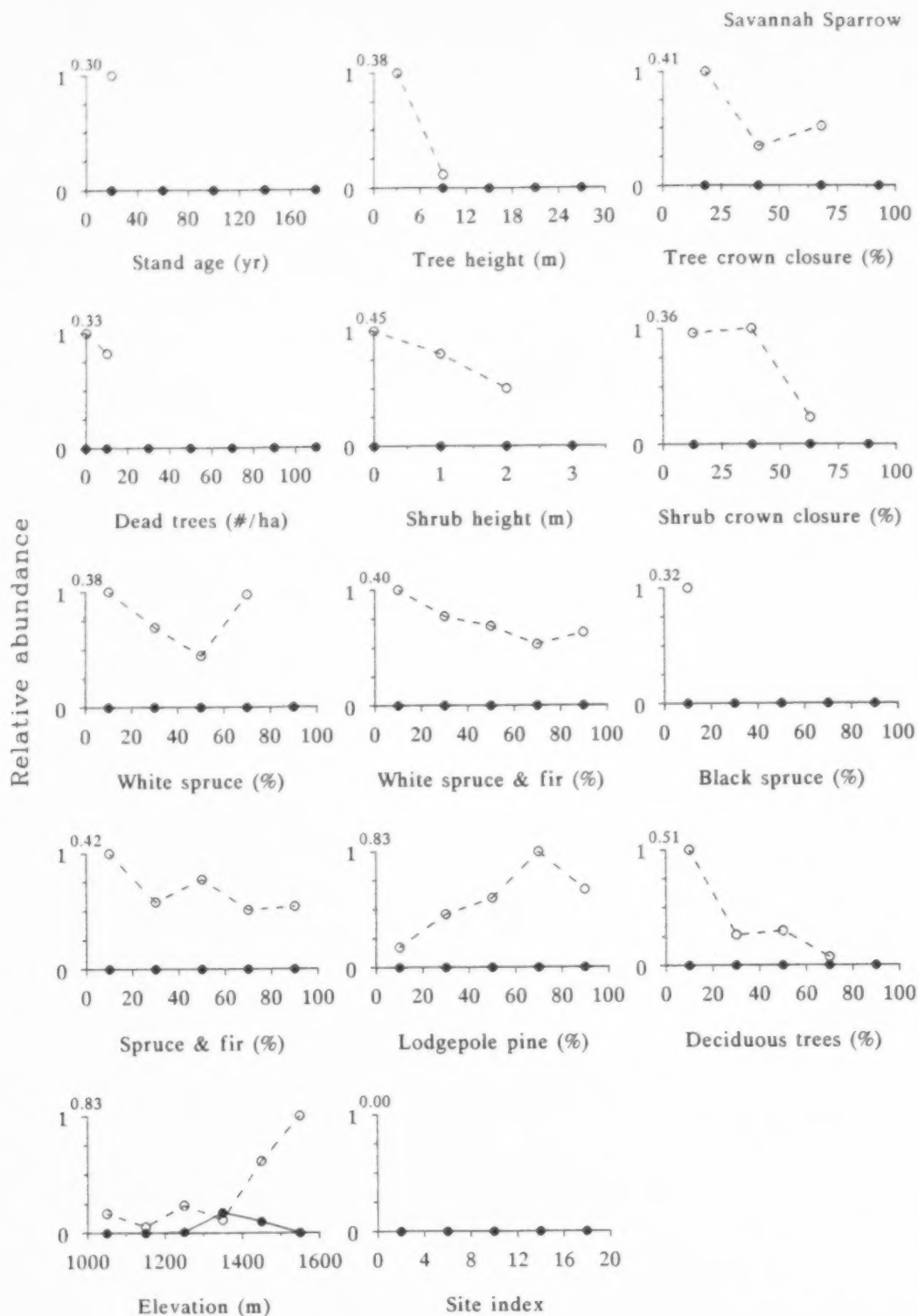
Hermit Thrush



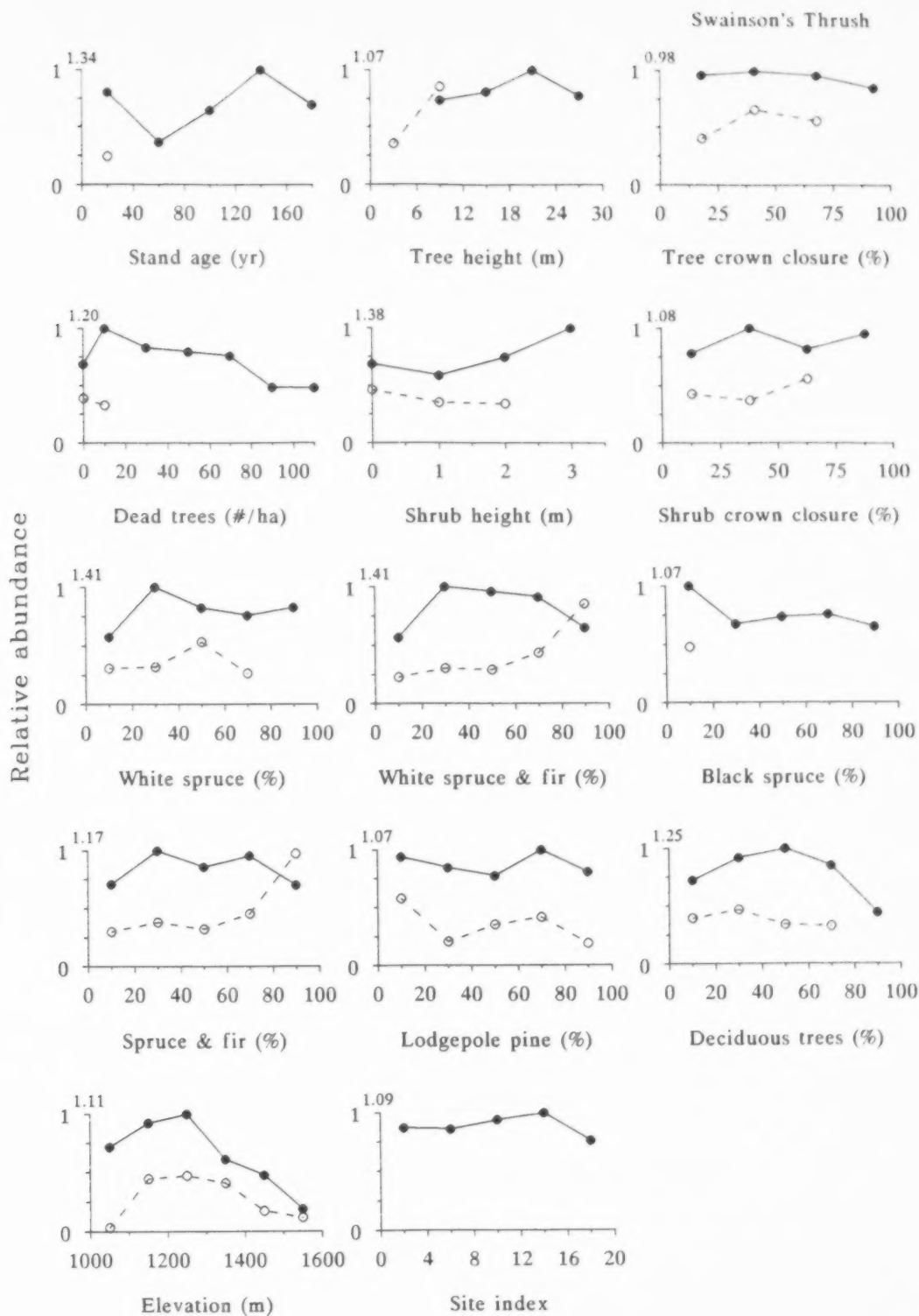
Appendix 4, continued. Relationships between abundance and habitat values for Hermit Thrush.



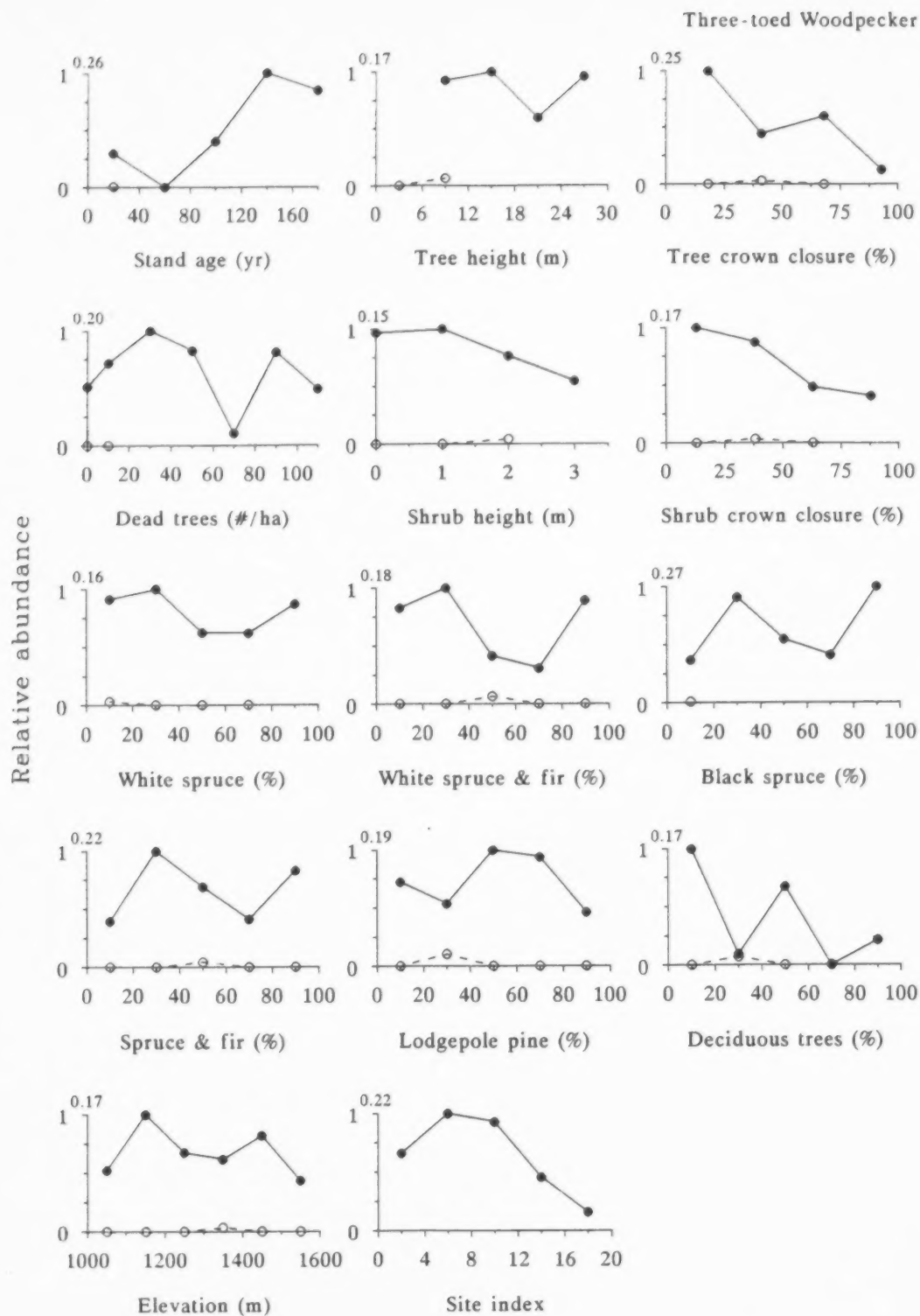
Appendix 4, continued. Relationships between abundance and habitat for Red-breasted Nuthatch.



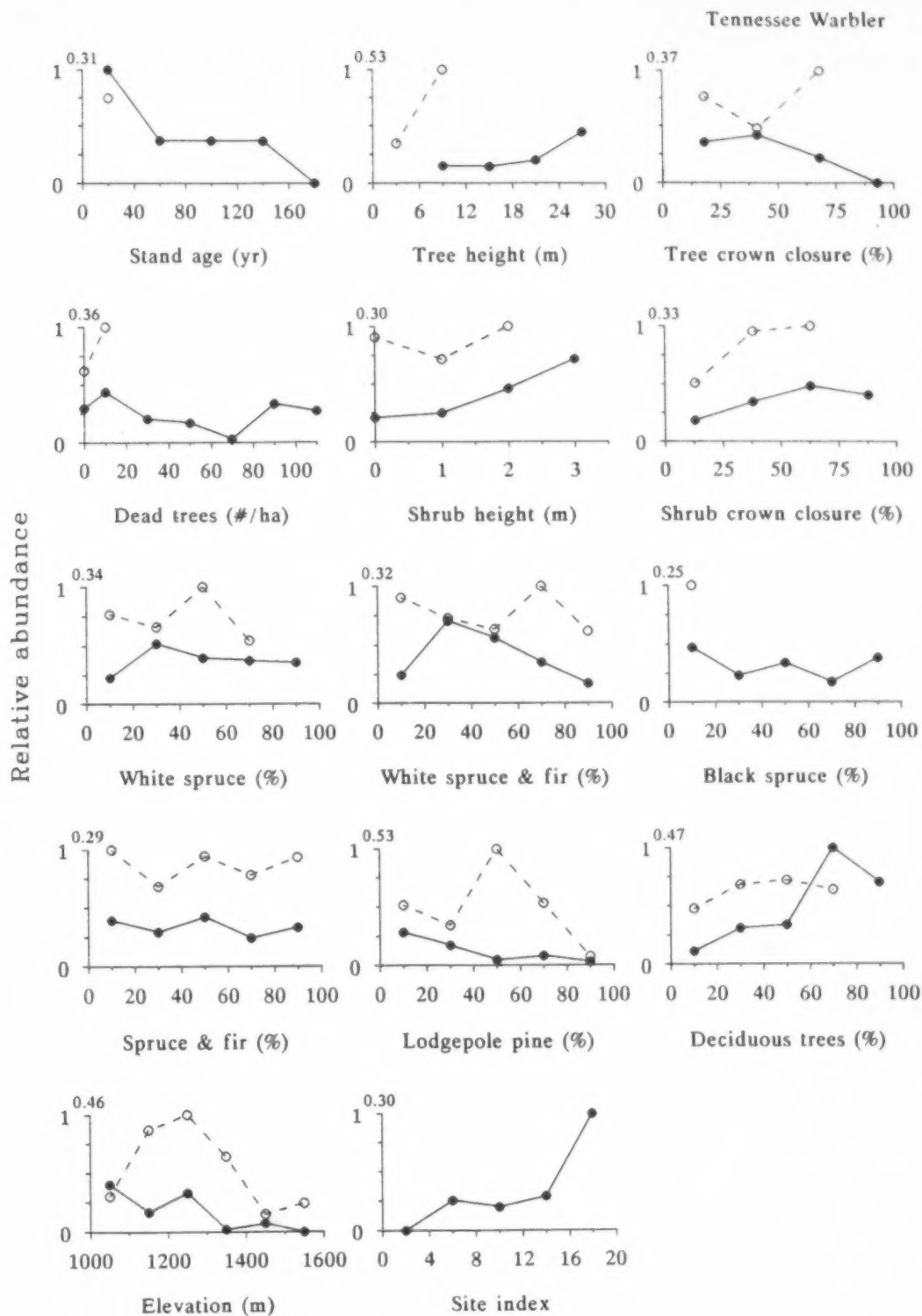
Appendix 4, continued. Relationships between abundance and habitat values for Savannah Sparrow.



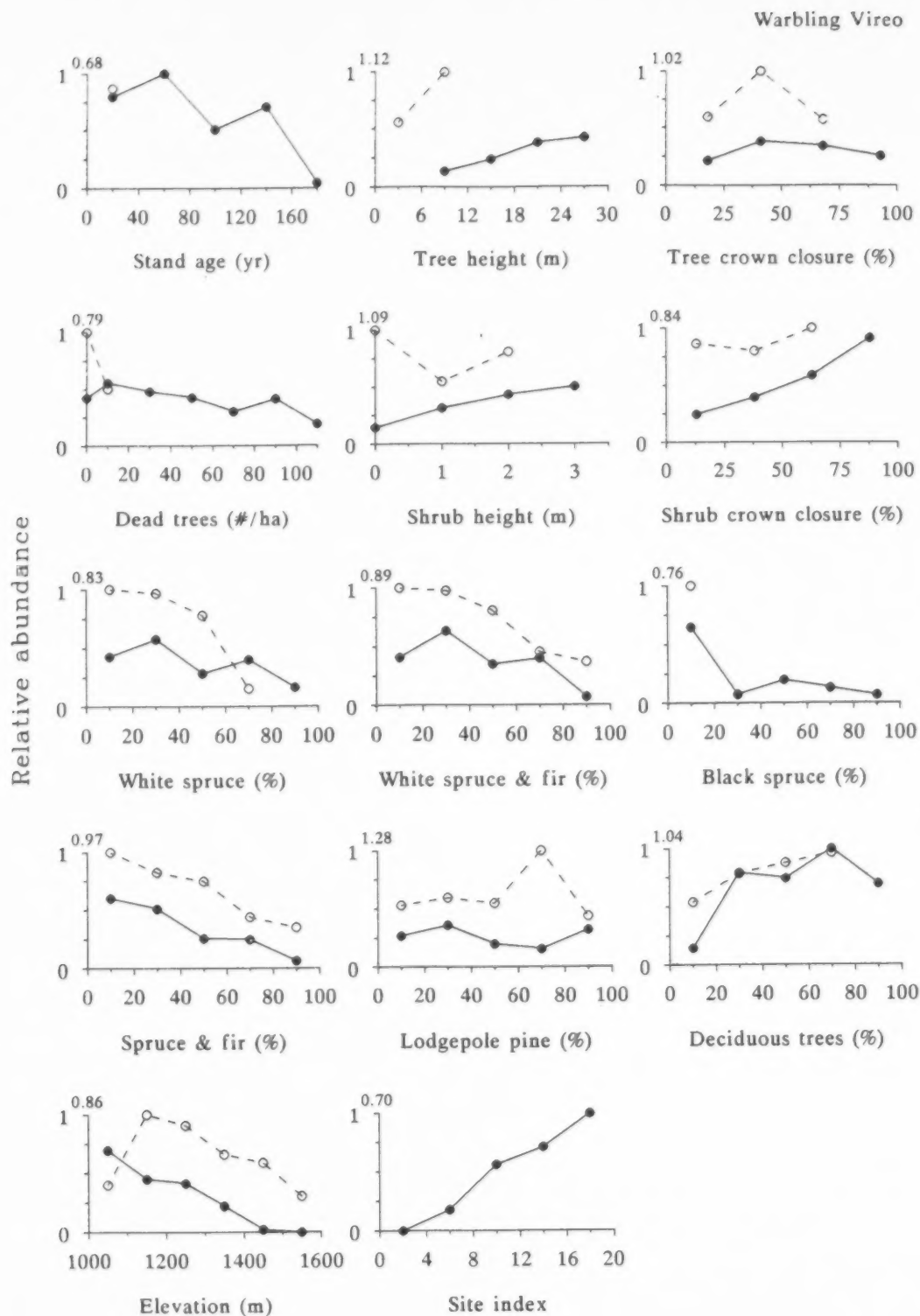
Appendix 4, continued. Relationships between abundance and habitat values for Swainson's Thrush.



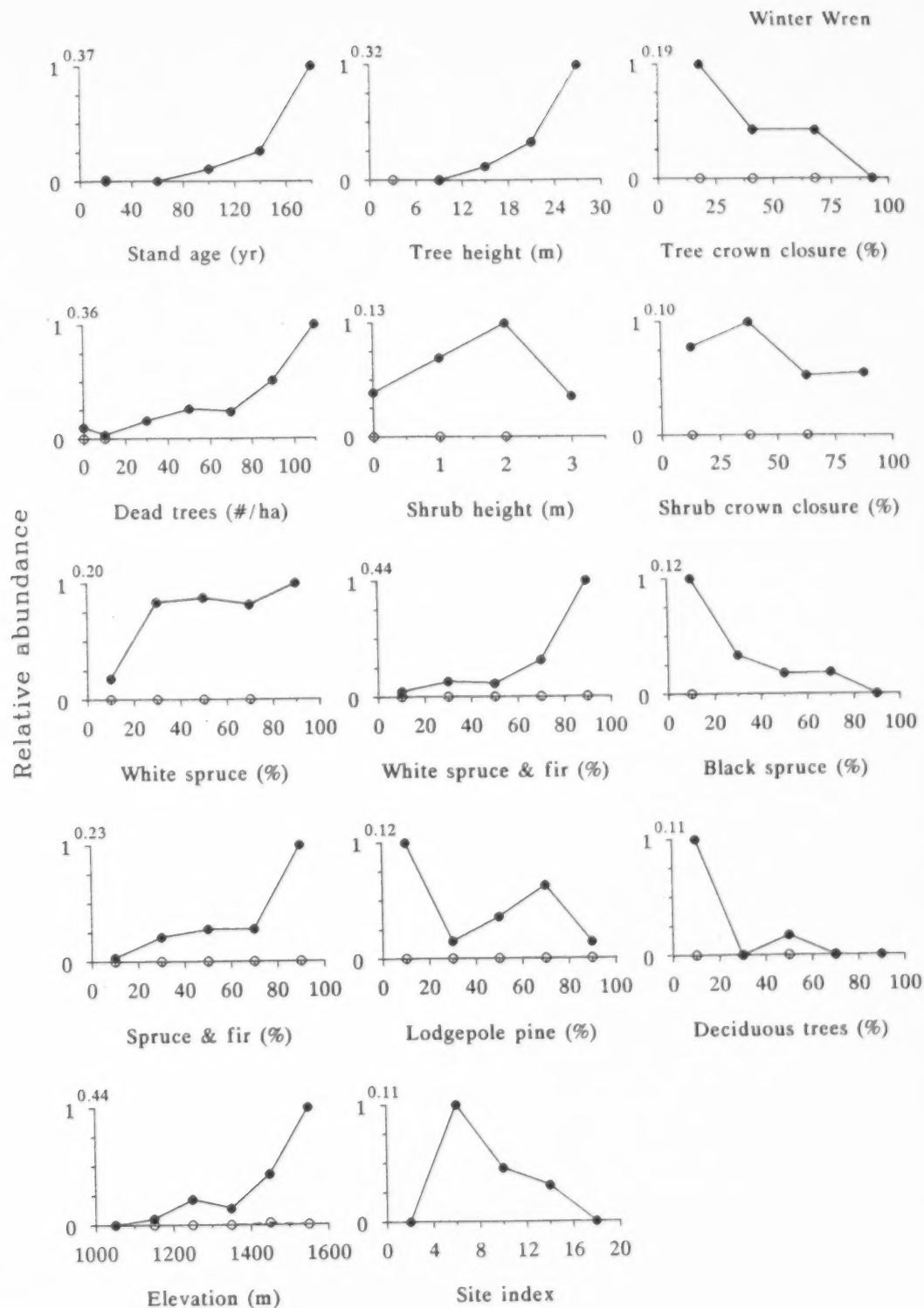
Appendix 4. Relationships between abundance and habitat for Northern Three-toed Woodpecker.



Appendix 4, continued. Relationships between abundance and habitat values for Tennessee Warbler.



Appendix 4, continued. Relationships between abundance and habitat values for Warbling Vireo.



Appendix 4, continued. Relationships between abundance and habitat values for Winter Wren.